SCALING EELGRASS COMPLEXITY IN NEWMAN SOUND, NEWFOUNDLAND AND APPLICATIONS TO FISH ECOLOGY

NADINE J. WELLS

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SCALING EELGRASS COMPLEXITY IN NEWMAN SOUND, NEWFOUNDLAND AND APPLICATIONS TO FISH ECOLOGY

by

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Abstract

Problems in ecology often exist at the scale of decades and large ecosystems while most variables can only be measured directly in small areas and over short periods of time. Therefore, multi-scale spatial analyses have become progressively more prevalent in ecological studies. Habitat, and the way in which organisms are distributed with respect to habitat, varies with scale both spatially and temporally. Eelgrass (*Zostera marina*) habitat, which grows in complex structural arrangements in marine environments, has been shown to enhance the diversity and density of invertebrate and vertebrate species, including juvenile Atlantic cod (*Gadus morhua*) in Newfoundland. Eelgrass exhibits a hierarchical arrangement of spatial structure suggesting that area and complexity measures may not scale isometrically. I obtained scaling laws for eelgrass habitat area and perimeter using two sources: underwater video along transect lines (small scales) and aerial photographs (large scales). I determined that a common scaling law for eelgrass habitat holds at small and large scales if lateral heterogeneity within a site is insignificant. Also, fractal dimensions were used as a measure of complexity for eelgrass habitat at 8 sites where age 0 Atlantic cod were collected by beach seine. In a two-phase analysis, I first determined that cod were more likely to be caught at eelgrass sites exhibiting high complexity during early months of recruitment (i.e., July and August) whereas they were found equally at all sites later in the season (i.e., September through November). In the second phase, it was determined that when cod were present, the relationship with eelgrass complexity was strong only in September, with cod being found in highest densities at intermediately complex eelgrass sites. Relationships between cod density and eelgrass complexity for all other months and years were not consistent indicating that factors other than eelgrass complexity had a greater influence on the distribution of cod during these months. I have confirmed that incorporating scale into ecological studies is important and that studies should be carried out at scales appropriate to the questions being posed.

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Chapter 1: Introduction and Overview

Multi-scale spatial analyses have become progressively more prevalent in ecological studies (Schneider 2001). This is because problems in ecology often exist at the scale of decades and large ecosystems while most variables can only be measured directly in small areas and over short periods of time. Investigators have become aware that patterns measured at small scales do not necessarily hold at larger scales (Turner 1989; Schneider 2001) and that the scale at which studies are designed has a substantial impact on results obtained (Dayton and Tegner 1984; Wiens 1989; Farmer and Adams 1991; Gardner 1998). Many investigators (e.g., Farmer and Adams 1991; Hewitt et al. 1998; Schneider et al. 1997b; Thrush et al. 1997) suggest multi-scale studies to resolve issues of scale.

Habitat, and the way in which organisms are distributed within it, varies both spatially and temporally with scale. Historically, multi-scale studies of habitat focused on terrestrial systems (see Robbins and Bell 1994). Aspects of aquatic habitats, such as type (Ross et al. 1997), biomass (Adams 1976a; Orth and Heck 1980) areal extent (Gibson 1994; Miranda and Pugh 1997), plant structure (Orth et al. 1984), ecological efficiency (Adams 1976b) and latitude (Nelson 1980), influence the distribution and behavior of organisms. However, these studies have excluded the notion of scale. Contemporary research has focused on the influence of edge (Baltz et al. 1993), density (Bell and Westoby 1986a; Carr 1994; Graham et al. 1998), spatial configuration (Irlandi et al. 1995; Irlandi 1997), fragmentation (Dunham et al. 1997), or complexity (Heck and Orth 1980; Gotceitas and Colgan 1989; Mattila 1992) of habitat on organisms and ecological

processes; but again, these studies do not incorporate scale explicitly. Habitat patterns found at small spatial scales may be very different from those found at broader spatial scales (Wiens 1989). Thus, studies identifying scale-dependent relationships between organisms and aquatic habitat are becoming more prevalent (Bell and Westoby 1986b; Gee and Warwick 1994; Syms 1995; Davenport et al. 1996; Azovskii and Chertoprud 1997; Beck 1998; Connell and Kingsford 1998; Palacín et al. 1998; Snover and Commito 1998; Muotka et al. 1998; Turner et al. 1999; O 2002).

Seagrass communities are distributed along temperate coasts worldwide. Eelgrass (*Zostera marina*) is the most wide-spread species, having a distribution in the northern portions of the Pacific and Atlantic oceans, extending into the Arctic seas (den Hartog 1971). Eelgrass occurs as dense beds in tidal and subtidal areas (Rasmussen 1977) with substrates varying from soft mud to gravel mixed with coarse sand (Tutin 1942). Eelgrass anatomy, growth, and reproduction are described by Tutin (1942) and Rasmussen (1977). A plant consists of a more or less vertically growing group of leaves collected in a shoot which produces four to six bandlike leaves per year. The leaves arise from a horizontal perennial rootstock, a rhizome, supplied with bundles of roots. The flowers are formed on a separate erect stem and are fertilized by waterborne pollen. Vegetative reproduction by rhizome growth also occurs, and under most marine conditions probably plays a more dominant role than sexual reproduction. However, vegetative reproduction is of limited duration and is dependent on light availability and temperature.

Seagrass communities have a number of functions that have been reviewed extensively elsewhere (Wood et al. 1969; den Hartog 1977; Kikuchi and Pérès 1977;

Kikuchi 1980; Thayer et al. 1984). The main functions of seagrass (i.e., eelgrass) can be summarized as follows:

1. The long blades reduce water movement by currents and waves, offering a calm underwater space within it (Kikuchi and Pérès 1977; Kikuchi 1980; Fonseca et al. 1982).
2. Velocity reduction increases the accumulation of inorganic and organic material and reduces turbulence and scouring (Wood et al. 1969; Kikuchi 1980; Thayer et al. 1984). Though sediment-trapping is one of the general features of seagrass beds, rhizomes of *Zostera marina* only grow horizontally (as opposed to upright) and this sediment-trapping action is less obvious (Kikuchi and Pérès 1977; Kikuchi 1980).
3. This habitat serves to reduce erosion, stabilize the bottom substrate, and preserve sediment microflora, resulting from its gregarious growth and dense root system (den Hartog 1977; Thayer et al. 1984; Wood et al. 1969).
4. By photosynthetic activity, seagrasses produce oxygen and consume CO_2 dissolved in the water during the daytime (Kikuchi and Pérès 1977). High O_2 concentration in the seagrass bed can support high densities of various animal forms in proximity to highly organic reducing substrates (Kikuchi and Pérès 1977).
5. The leaf canopy diminishes illumination in the daytime, protecting the bottom from strong insolation and permitting a shaded microenvironment to develop at the base of the vegetation (Kikuchi and Pérès 1977; Kikuchi 1980). When the

intertidal seagrass bed is exposed to the air, leaves cover the bottom surface and protect their inhabitants against strong sunlight and minimize the fluctuation of temperature and salinity (Kikuchi and Pérès 1977).

6. Plants and detritus production influence nutrient cycling between sediments and overlying waters (Wood et al. 1969) and provide a significant and long-term source of nutrients for sediment microheterotrophs (Thayer et al. 1984). In addition, movement of water and fauna transports living and dead organic matter (particulate and dissolved) out of eelgrass meadows to adjacent systems (Thayer et al. 1984).
7. Eelgrass increases available substrate surface for epiphytic algae and associated fauna (Wood et al. 1969; Kikuchi and Pérès 1977; Kikuchi 1980), with as much as 20 times more surface area for small sessile flora and fauna as compared to unvegetated areas (McRoy and Helfferich 1980). Also, the differentiation of the plant body into leaves, stems and rhizomes increases the diversity of microhabitats, and as a result, it supports a great diversity of animals that do not feed directly upon the eelgrass (Kikuchi and Pérès 1977; Kikuchi 1980).
8. One of the most important functions of eelgrass is to provide a structural habitat or shelter to a variety of organisms (den Hartog 1977) by the variety of living spaces in the vertical and horizontal structure of the grass bed itself (Thayer et al. 1984). In this sense, it acts as a nursery to shellfish, crustaceans, and many juvenile and adult fishes. Roots and leaves provide horizontal and vertical complexity which, coupled with abundant and varied food resources, leads to

densities of sessile and mobile fauna generally exceeding those in unvegetated habitats (Thayer et al. 1984). There are more hiding places which attract prey leading to high local concentration of prey for predators to eat (McRoy and Helfferich 1980).

9. A variety of primary and secondary sources of organic carbon are present in eelgrass communities that provide multiple food resources for invertebrates and vertebrates (Thayer et al. 1984). Eelgrass is digested by a very restricted number of organisms (Wood et al. 1969; den Hartog 1977; Kikuchi and Pérès 1977; Kikuchi 1980). However, leaves produce large quantities of organic material that decomposes within the meadow and becomes available to bottom fauna via detritus (den Hartog 1977; Kikuchi and Pérès 1977) or is transported to adjacent systems (Wood et al. 1969). Once washed ashore and decomposing, this detritus is eaten by several species of insect (den Hartog 1977).

Eelgrass habitat has been shown to positively enhance the diversity and density of invertebrate and vertebrate species relative to non-vegetated areas. Orth et al. (1984) summarize studies describing the influence of seagrass plant architecture on associated animal distributions and abundance. Orth and Heck (1980) found that fish abundance and species number increased as water temperature and eelgrass biomass increased. Adams (1976b) found that eelgrass systems have high ecological efficiencies indicating that eelgrass beds are efficient systems for converting consumed energy and solar radiation into fish biomass.

Eelgrass systems also protect organisms from predation. Eelgrass features such as shoot density, grassbed patchiness, plant biomass, individual leaf area, leaf morphology and the thickness, structure and proximity of the rhizome layer to the sediment surface, can potentially mitigate the effects of predation (Orth et al. 1984). However, the relationship between some of these characteristics and predator success does not appear to be linear (Orth et al. 1984). Instead, a threshold level of these plant characteristics seems necessary for significant protection from predation to occur (Nelson 1979; Heck and Thoman 1981; Crowder and Cooper 1982; Savino and Stein 1982). Graham et al. (1998) found a decreasing exponential relationship between feeding efficiency of mummichogs and eelgrass shoot density. They attributed the higher abundance of fish in eelgrass beds compared to unvegetated habitats to greater food availability because invertebrates benefit from the protection of eelgrass as well. Gotceitas and Colgan (1989), using artificial vegetation similar to eelgrass, found a non-linear relationship between increasing plant stem density and predator (largemouth bass) foraging success. They also found a positive non-linear relationship between increasing habitat complexity (plant stem density) and prey (juvenile bluegill sunfish) choice of habitat. Irlandi et al. (1995) demonstrated that the rates of predation on an epifaunal bivalve increased with increasing fragmentation of seagrass habitat. These results indicate that seagrass structural patterns have a major effect on the organisms associated with them.

In Newfoundland, juvenile Atlantic cod (*Gadus morhua*) are often associated with eelgrass (Gotceitas et al. 1997). Adult Atlantic cod spawn in the deep waters of the continental shelf (offshore stocks) and within inshore bays ("bay stocks") usually

between April and June (Scott and Scott 1988). The number of eggs spawned can range from 200 thousand to 12 million per individual, depending on female size (Scott and Scott 1988). The fertilized eggs float with currents until they hatch as small (3-6 mm) larvae (Scott and Scott 1988). The larvae develop into pelagic (0+ yr) juvenile cod that settle after 2-4 months into demersal habitats where ambient temperatures are often less than 10°C. In cold waters influenced by the Labrador Current, settlement often occurs in shallow (4-7 m) water along Newfoundland's east coast (Methven and Schneider 1998).

Juvenile cod are widely distributed throughout both the inshore and offshore environments of Newfoundland and Labrador (Dalley and Anderson 1997). However, the cod stock off the east coast of southern Labrador and Newfoundland has been under a moratorium on commercial fishing since July 1992 (Shelton and Healey 1999). Understanding the ecology of juvenile cod in Newfoundland has been the focus of a number of recent studies (Gotceitas and Brown 1993; Methven and Bajdik 1994; Gotceitas et al. 1995; Fraser et al. 1996; Dalley and Anderson 1997; Gotceitas et al. 1997; Ings et al. 1997; Schneider et al. 1997a; Methven and Schneider 1998; Shelton and Healey 1999; Linehan et al. 2001; Gorman 2002; O 2002). Gaining insight into how cod are distributed relative to particular habitat types is an important part of understanding their ecology.

Post-settled (age 0+) Atlantic cod are associated with structurally complex habitats (Tupper and Boutilier 1995). They settle mainly in shallow sheltered areas and are often absent at exposed locations and in deep water (Godø et al. 1989). Moreover, juvenile cod show the ability to assess their surroundings and choose between habitat

types. In laboratory experiments, Gotceitas and Brown (1993) found that, with no apparent risk of predation, juvenile cod preferred sand or gravel-pebble substrate but when predators were present, cod utilized the interstitial spaces of cobble. Similar results were obtained by Fraser et al. (1996) on tests with age 0+ and age 1+ cod. Moreover, Gotceitas et al. (1995) found that when cod were exposed to an actively foraging predator, they hid in cobble or, when cobble was not available, in kelp. This behavior significantly reduced predation risk in both habitats. They suggested that juvenile cod are capable of assessing predator risk and adjust their response accordingly. Field observations have shown that juvenile cod may be associated with fleshy macroalgae (Keats et al. 1987), which the investigators suggested is used mainly for cover and, to a lesser degree, for food obtained from the algae. Recently, eelgrass has received more attention than other bottom cover types by investigators interested in juvenile cod habitat. Gotceitas et al. (1997) combined field and laboratory techniques to determine that eelgrass is used as a nearshore habitat by age 0+ cod and that latency until a predator captures an age 0+ cod increases with both the presence and density of vegetation. However, investigators have not been able to find a relationship between cod abundance and eelgrass cover (Norris et al. in prep). Limitations on suitable habitat availability, such as physical abundance and occupance by competitors (Fraser et al. 1996), may also affect the distribution and survival of juvenile cod (Lough et al. 1989; Tupper and Boutilier 1995).

Studies consistently show that age 0 cod abundance declines in vegetated sites at night while the reverse is true at non-vegetated sites (Borg et al. 1997; Linehan et al.

2001). Borg et al. (1997) suggested that availability of vegetation during the day as a predation refuge, as well as open areas for feeding during night, seems to be important for juvenile cod. I hypothesized that eelgrass habitat with intermediate complexity (as measured by area and perimeter) would be most suitable for cod (hereafter referred to as the "intermediate optimum hypothesis"). Eelgrass habitat low in complexity would have too little edge, possibly leading to decreased access to food. Gorman (2002) found that predation risk for age 0 cod was greatest at the edge of eelgrass habitat compared to surrounding bare areas or eelgrass habitat. This risk decreased as distance from the edge increased. Therefore, I expect eelgrass habitat high in complexity to be less suitable than eelgrass with intermediate complexity because it has too much edge.

Eelgrass is one of several species of seagrass that grows in complex structural arrangements in marine environments. It exhibits a hierarchical arrangement of spatial structure, ranging from millimeters to kilometers: from rhizomes and shoot groups, to discrete patches of eelgrass, to eelgrass meadows (Robbins and Bell 1994; Turner et al. 1999). Meadows may be extensive and continuous or highly fragmented and arranged in a mosaic of small patches (Robbins and Bell 1994). Seagrass patterns are apparently controlled by factors such as major storms, bottom geology and morphology, and light penetration (Kelly 1980). Wind-generated wave dynamics, tidal currents and water depth are also important influences on the spatial configuration of seagrass beds, both through direct control of bed development, as well as through alteration of bed heterogeneity or patchiness (Turner et al. 1999).

Several investigators have measured components of seagrass habitat structure, including patch size (Irlandi 1997), shoot density (Bell and Westoby 1986a; Graham et al. 1998), biomass (Adams 1976a), and leaf height (Bell and Westoby 1986a). However, complexity of seagrass habitat based on spatial patterning has rarely been quantified (but see Turner et al. 1999 and O 2002). Investigators have often referred to surrogate measures of complexity such as leaf height or density (e.g., Bell and Westoby 1986a; Gotceitas and Colgan 1989; Graham et al. 1998). Alternatively, measurements of spatial patterning of habitat structure have been made, but only at one scale (Irlandi et al. 1995). Techniques developed for terrestrial landscapes, such as scaling laws or fractal analyses (Sugihara and May 1990; Williamson and Lawton 1991), can be applied to measure the complex spatial patterning of seagrasses at several scales.

Fractal geometry has been a useful tool in ecological sciences for quantifying aspects of habitat over multiple spatial scales (Sugihara and May 1990; Hastings and Sugihara 1993; Johnson et al. 1995; Kenkel and Walker 1996). Fractal analyses relate some dimension of habitat to the scale at which it is measured and provide a numerical expression of complexity independent of the nature of that habitat (Gee and Warwick 1994). This type of analysis has been used to determine spatial patterns in landscapes (Burrough 1981; Krummel et al. 1987; Milne et al. 1992; Otto 1996; Ritchie 1998; Nikora 1999), ecological habitats (Williamson and Lawton 1991; Solé et al. 1994), and vegetation (Morse et al. 1985; Palmer 1988; Scheuring and Riedi 1994; van Hees 1994). The majority of fractal studies are based on terrestrial systems. However, fractal analyses are becoming common in aquatic systems as well (Gee and Warwick 1994; Simon and

Simon 1995; Azovskii and Chertoprud 1997; Snover and Commito 1998; Turner et al. 1999).

Studies quantifying eelgrass complexity have used different methods at different scales (e.g., Turner et al. 1999; O 2002). In New Zealand, aerial photographs at scales of 1:1500 and 1:3000 were used to determine seagrass complexity by way of fractal analyses (Turner et al. 1999). In Newfoundland, O (2002) analyzed imagery collected using a Compact Airborne Spectrographic Imager (CASI) to determine a scaling law comparing perimeter-to-area ratios of eelgrass habitat over a range of resolutions. This enabled her to quantify the complexity of eelgrass habitat structure as a function of spatial scale. She found consistent values for the exponent of the scaling law over spatial scales spanning two orders of magnitude. This indicates that large-scale structural complexity is simply a magnified version of small-scale complexity within this range of spatial scales. Thus, eelgrass area and perimeter measurements taken using finer resolutions (e.g., aerial photography and underwater video) should provide information to extend scaling laws to these resolutions.

Investigators addressing the same questions have often conducted studies at quite different scales, resulting in conflicting findings (Wiens 1989). I set out to determine if measurements of eelgrass area and perimeter made at small scales (as measured from underwater video) would have similar scaling relationships as measurements made at larger scales (as measured from aerial photographs). I compared several resolutions of eelgrass measurements from underwater transect video to several resolutions of measurements from aerial photographs to determine if a common scaling law for eelgrass

habitat would hold at small and large scales. In a second study, using measurements of area and perimeter of eelgrass habitat, I determined complexity using fractal analyses. To determine if age 0 Atlantic cod are influenced by structural complexity of habitat, I analyzed cod density data in relation to eelgrass complexity.

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Co-authorship Statement

Chapter 2: A multi-scale analysis of eelgrass spatial patterns

Nadine Wells designed and identified the research proposal, aided in the collection of all field and computational data, performed the data analysis, and prepared the manuscript. David C. Schneider contributed with development of ideas, methods and statistical analyses. Robert S. Gregory organized and helped with the acquisition of aerial photographs and underwater video. Danny W. Ings aided with statistical analyses and contributed to the development of the manuscript. All co-authors contributed to editing of the manuscript.

Chapter 3: Influence of the spatial complexity of eelgrass (*Zostera marina*) on age 0 Atlantic cod (*Gadus morhua*) densities

Nadine Wells designed and identified the research proposal, aided in the collection of all field and computational data, performed the data analysis, and prepared the manuscript. David C. Schneider contributed with the development of ideas, and statistical analyses. Robert S. Gregory helped with and organized fieldwork, including the acquisition of aerial photographs and fish density data. Danny W. Ings aided with statistical analyses and contributed to the development of the manuscript. All co-authors contributed to editing of the manuscript.

Chapter 2: A multi-scale analysis of eelgrass spatial patterns

2.1 Introduction

In ecological research, problems often exist at temporal scales of decades and spatial scales of large ecosystems, whereas most variables can only be measured directly in small areas, over short periods of time. In order to effectively conduct research, one must undertake studies at scales relevant to the problem (Wiens 1989; Farmer and Adams 1991; Gardner 1998), which is tricky because patterns measured at small scales do not necessarily hold at larger scales (Turner 1989; Levin 1992; Schneider 2001). Many investigators (e.g., Farmer and Adams 1991; Hewitt et al. 1998; Schneider et al. 1997; Thrush et al. 1997) have noted the importance of scale and have suggested that to solve scale-dependent problems, multi-scale studies be done whenever possible.

Habitat, and more specifically, vegetation patterns, vary spatially and temporally depending on scale. Patterns found at small spatial scales may be very different from those found at broader spatial scales (Wiens 1989). Information is lost as spatial data are considered at coarser scales of resolution (Schneider and Piatt 1986; Turner 1990). Thus, the development of methods that preserve information across scales is critical (Turner 1990). Several studies (Conner and Bowers 1987; Farmer and Adams 1991; Ritchie 1998; Nikora et al. 1999) have shown that habitat can and should be measured at several scales, with the range depending on the processes being investigated. When habitat complexity or heterogeneity is measured at numerous scales, scaling laws or fractal analyses are often used (Gee and Warwick 1994; Otto 1996), thus permitting estimations

at any scale. Fractal analyses relate some dimension of habitat to the scale at which it is measured. Fractal analyses have been used to describe spatial patterns of various types of terrestrial (Krummel et al. 1987; Palmer 1988; Scheuring and Riedi 1994; van Hees 1994; Otto 1996) and aquatic vegetation (Gee and Warwick 1994; Azovskii and Chertoprud 1997), including seagrasses (Turner et al. 1999).

Seagrass habitat exhibits a hierarchical arrangement of spatial structure, ranging from millimeters to kilometers: from rhizomes and shoot groups, to discrete patches of eelgrass, to eelgrass meadows (Robbins and Bell 1994; Turner et al. 1999). Seagrass occurs naturally in a variety of complex but regular patterns, apparently controlled by such factors as major storms, bottom geology and morphology, and light penetration (Burrell 1977; Kelly 1980). Wind-generated wave dynamics, tidal currents and water depth are all important factors that influence the spatial configuration of seagrass beds, both through direct control of bed development, as well as through alteration of bed heterogeneity or patchiness (Turner et al. 1999). Eelgrass (*Zostera marina*) is one of several species of seagrass that grows in complex structural arrangements in Newfoundland waters. Factors influencing the spatial complexity of eelgrass beds have not been studied in Newfoundland.

Studies that have quantified eelgrass complexity have used different methods at different scales (e.g., Turner et al. 1999; O 2002). In New Zealand, aerial photographs at scales of 1:1500 and 1:3000 were used to determine seagrass complexity by way of fractal analyses (Turner et al. 1999). Using CASI (Compact Airborne Spectrographic Imager) imagery, O (2002) determined a scaling law comparing perimeter-to-area ratios

of eelgrass habitat over a range of resolutions, enabling her to quantify the complexity of eelgrass habitat structure as a function of spatial scale. She found consistent values for the exponent of the scaling law over spatial scales spanning two orders of magnitude. This pattern indicates that large-scale structural complexity is simply a magnified version of small-scale complexity within this range of spatial scales (O 2002). Thus, scaling laws should be extendable between measurements of eelgrass area and perimeter taken at coarse (e.g., aerial photography) and fine (e.g., underwater video) resolutions.

The box counting method is commonly used to quantify habitat structure as a function of spatial scale (Sugihara and May 1990; Hastings and Sugihara 1993; Kenkel and Walker 1996; Ricotta 2000). This method involves counting the number of boxes containing some characteristic of habitat (e.g., area or perimeter) in grids of decreasing resolution then regressing these counts against box size to obtain a scaling exponent. A derivation of this method involves calculating perimeter and area at each scale (Sugihara and May 1990). By regressing log area or log perimeter measurements at each scale against log resolution it is possible to obtain a scaling law that expresses change in area or perimeter as a function of scale. The area or perimeter can then be computed at any spatial measurement scale based on the scaling law.

Investigators addressing the same questions have often conducted studies at quite different scales, resulting in conflicting findings (Wiens 1989). I hypothesized that consistent results can be produced from analyses conducted at different scales. Specifically, I addressed the following question: do eelgrass area and perimeter measurements made at small scales have similar scaling relationships as measurements

made at larger scales? To answer this question, I measured eelgrass area and perimeter at 6 sites in Newman Sound using two methods: underwater transect line video and aerial photographs. Video data was taken at three transect lines (perpendicular to the beach) per site. Several scales of eelgrass measurements from transect video were then compared to several scales of measurements from aerial photographs to determine if a common scaling law for eelgrass habitat would hold at small and large scales.

2.2 Methods

2.2.1 Study area

Newman Sound is a fjord, 41 km long and 1.5 - 3.0 km wide, located in southwestern Bonavista Bay (Figure 2.1), on the northeastern coast of Newfoundland, Canada (48°35' N, 53°55' W). It is divided into two basins by a sill located ~7 km from the head of the sound, which rises to a depth of 18 m. The inner sound has a maximum depth of 55 m. The greatest depth of the outer sound is approximately 300 m at its seaward end. For a detailed description of bottom substrates in the fjord, see Linehan et al. (2001).

I selected 6 sites (Figure 2.1) based on the presence and spatial configuration of eelgrass habitat. Eelgrass was associated with mud, silt, sand, and gravel substrates and, where present, is generally restricted to depths of less than 6 m in Newman Sound.

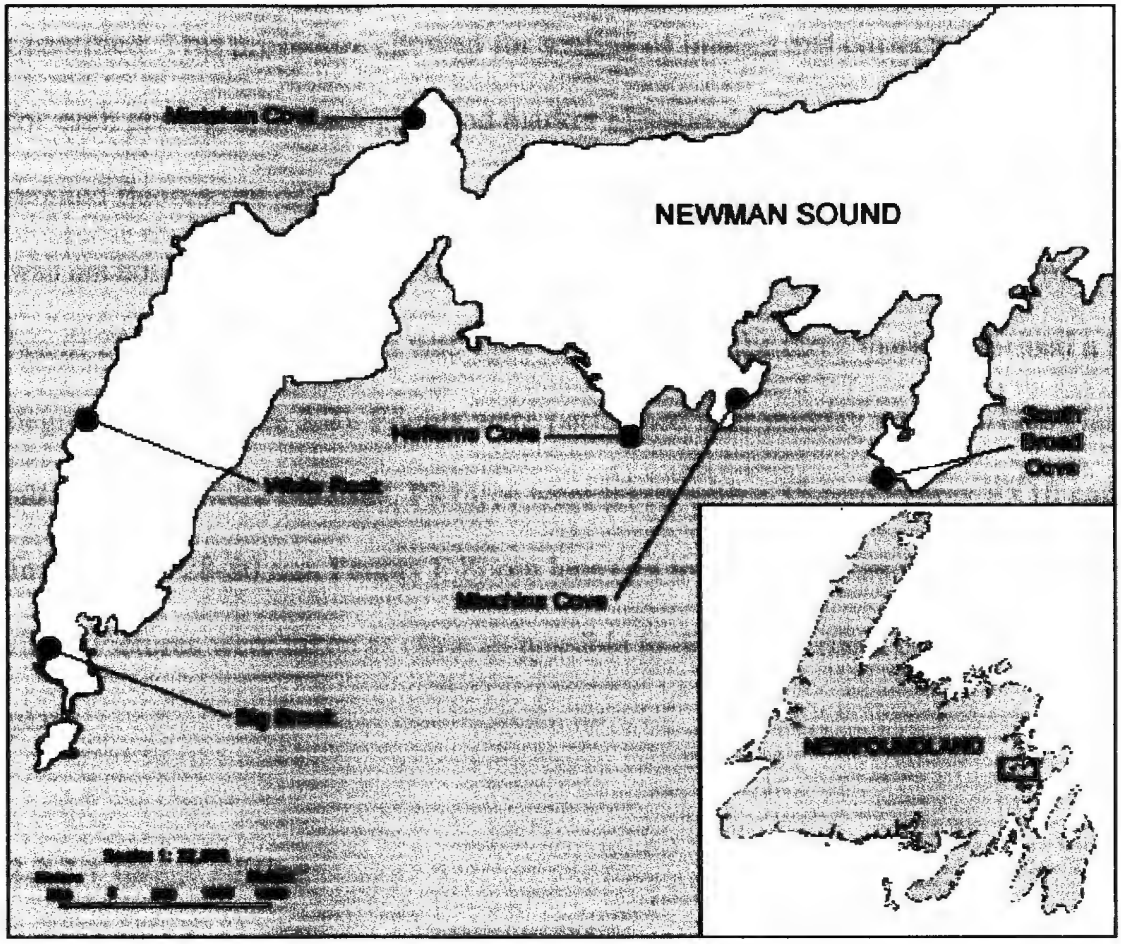

Figure 2.1: Map of the study area, Newman Sound, Newfoundland, showing the location of the 6 sites used in this study: Big Brook, White Rock, Mistaken Cove, Hefferns Cove, Minchins Cove, and South Broad Cove.

2.2.2 Aerial photography

Aerial photographs of the 6 sites were taken in August 2000 from a single-engine Cessna floatplane at altitudes between 150 m and 300 m. Prior to taking photographs, markers were set out at each site to delineate the area in which eelgrass habitat was to be quantified. This procedure allowed for scaling of images and correction of camera angle for each photograph. Each plywood marker measured 0.6 m x 0.6 m and was spray-painted fluorescent orange. One marker floated on the ocean surface 50 m offshore and was anchored with a rope tied to a concrete block. Two other markers were placed on the beach 25 m apart; a compass was used to ensure that the three markers formed a 90 degree angle (Figure 2.2). Flights were performed near midday when surface glare and surface winds were minimal. Pictures were taken with a 35-mm Pentax FX10 camera, fitted with a 28-80 mm Pentax F Zoom lens (set to 50 mm), haze filter, and polarizer filter. Pictures were taken as close as possible to directly vertical over the site to avoid glare.

2.2.2.1 Image editing

Aerial photographs were developed to a Kodak Digital Science Photo CD Master disc, with highest resolution level of 2048 x 3072 pixels. Images were edited using Adobe Photoshop 5.5. Each image was adjusted to bring the markers into 90° alignment, scaled using transformation features (skewing and scaling) in Adobe Photoshop, and cropped to represent 3600 m^2 (60m x 60m) on the ground (see Appendix 1).

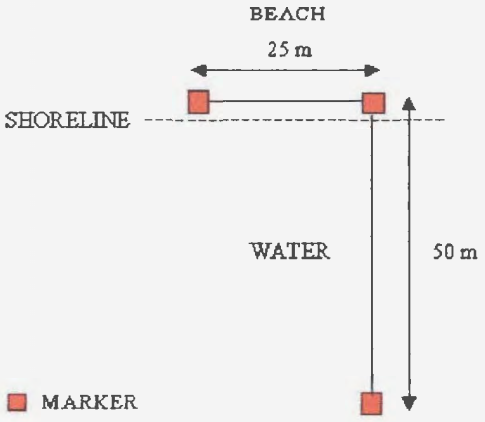

Figure 2.2: A depiction of the layout of markers at each site for purposes of scaling aerial photographs correctly. Onshore markers were 25 meters apart. The third marker was 50 meters offshore. All three markers formed a 90° angle.

2.2.2.2 Ground truthing

Before quantifying habitat from the aerial photographs, each site was ground surveyed using an aquascope (PVC with Plexiglas bottom). A rough map of each site was drawn with a general layout of habitat types (e.g., eelgrass, *Fucus*, mineral substrates), enabling verification of habitat types observed on the aerial photographs.

2.2.2.3 Box counting

I used a box-counting method (Sugihara and May 1990) to quantify eelgrass area and perimeter at several scales of resolution from the aerial photographs. A grid containing 3600 boxes (1 m^2 each on the ground) was placed over each digital aerial photograph. Two types of data from the image were transferred manually to printed replicas of the grid: presence or absence of: (1) eelgrass habitat (area measurement) and (2) eelgrass habitat edge (perimeter measurement). Once the area and perimeter data from the highest resolution grid were transferred, grids of lower resolution (i.e., fewer boxes) were placed over the 3600-box grid. The number of boxes containing area and perimeter were counted at resolutions of 1 m^2, 4 m^2, 9 m^2, 16 m^2, 25 m^2, 36 m^2, 100 m^2, 225 m^2, 400 m^2, and 900 m^2. Eelgrass habitat area was calculated by multiplying the number of boxes that contained eelgrass at a given resolution by the size (m^2) of the boxes. Eelgrass habitat perimeter was calculated by multiplying the number of boxes that contained perimeter at a given resolution by the length of a side (m) of a box.

2.2.3 Underwater video

Underwater video was taken in September 1999 along 3 transects at 6 sites. Transect lines were 100 m long and laid down perpendicular to the shore starting near the beach, separated by approximately 8 m. Two divers swam along the transect lines at a constant rate. One diver followed the transect line while the second diver held the video camera (H18 mm camcorder, Sony model V101, enclosed in a waterproof housing) at a 45° angle centered over the transect line.

2.2.3.1 Data extraction

Data was extracted from the underwater video along the 1 m wide x 100 m long transect strip using a timer. Video was played back on a computer and the amount of time during which eelgrass or no-eelgrass was visible was recorded. The average swimming rate in m/s was calculated by dividing 100 m by the total time it took to swim each transect line. Eelgrass habitat measurements were calculated by multiplying the average swimming rate by the amount of time that eelgrass and no-eelgrass habitats were visible. A scaled visual depiction of each transect line was created (Figure 2.3) and the "distance along transect" on the x-axis was cropped to 60 m to be comparable to the size of the aerial photographs. Transect lines (1 m wide) were split into bins of $60m^2$, $30m^2$, $15m^2$, $10m^2$, $5m^2$, $2m^2$, $1m^2$, $0.5m^2$, $0.2m^2$, and $0.1m^2$ for a total of ten scales of measurement. I quantified eelgrass habitat area by counting the number of bins that contained eelgrass at each scale and multiplying them by bin size (m^2) to obtain an area measurement (m^2) for each resolution. Perimeter measurements were made by counting the number of bins that

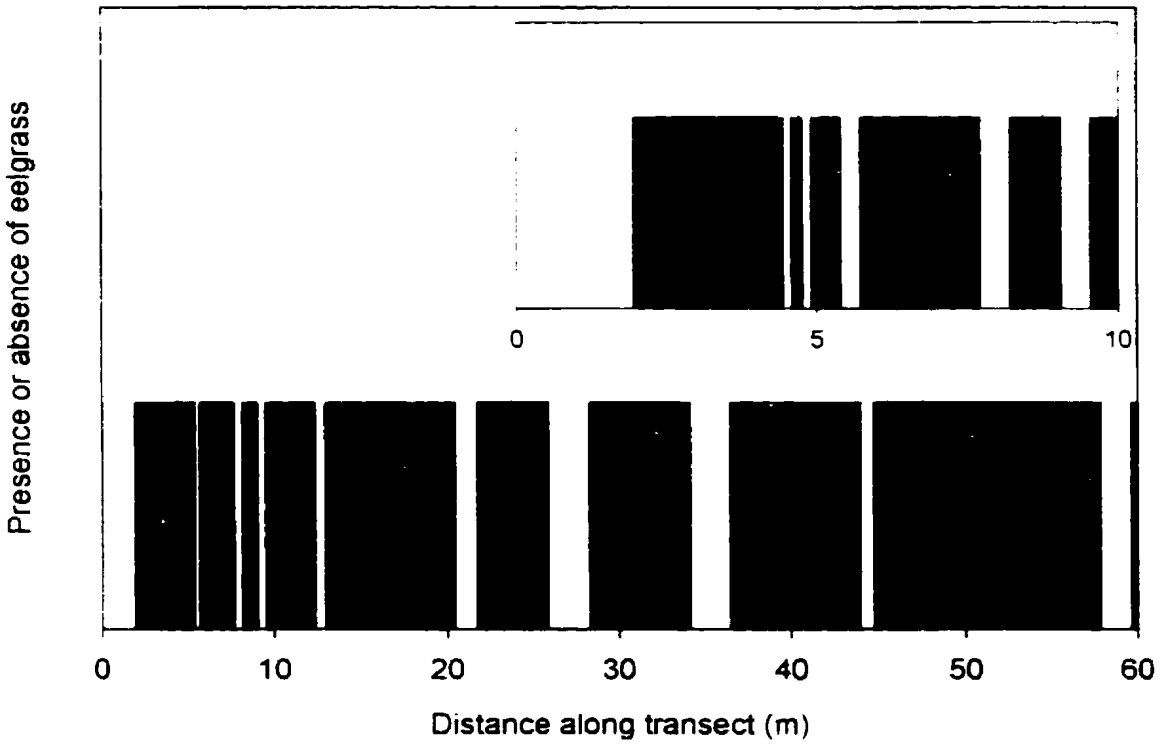

Figure 2.3: Depiction of eelgrass growth along middle transect line from Mistaken Cove. See inset for enlargement of 0 – 10 m section of the transect.

contained eelgrass habitat edge and multiplying by bin size (m) to obtain a perimeter measurement (m) for each resolution.

2.2.4 Test for lateral heterogeneity across transects

To determine if the same scaling relation held for area measurements across transect lines, I applied the following model for each site:

$$\log(A) = \log(R) + [\log(R)]^2 + L + \log(R)*L + [\log(R)]^2*L \qquad (2.1)$$

where A = area (m^2); R = resolution (bin size, m^2); and L = transect line (categorical variable where L = left, middle or right). I used a quadratic model because the relationship between log area and log resolution was not linear. If $[\log(R)]^2$ was not significant, the model was reduced to a linear model. If log(R)*L and/or $[\log(R)]^2*L$ were significant, scaling exponents were different for each transect line indicating that lateral heterogeneity existed across transect lines. A similar model was applied to determine if lateral heterogeneity existed across transect lines for perimeter:

$$\log(P) = \log(R) + [\log(R)]^2 + L + \log(R)*L + [\log(R)]^2*L \qquad (2.2)$$

where P = perimeter (m), R = resolution (bin size, m) and L = transect line.

All analyses were performed using SAS (1988). All models were based on a general linear model with a normal error structure. Tolerance of type I error was $\alpha = 0.05$. Residuals were examined for homogeneity, normality and independence.

2.2.5 Computing between scales

I compared scaling exponents computed for area and perimeter from underwater transect line data to scaling exponents computed for area and perimeter from aerial photograph data. Area data from all transect lines were averaged and compared to area data from aerial photographs for each site using the following model:

$$\log(A) = \log(R) + [\log(R)]^2 + M + \log(R)*M + [\log(R)]^2*M \qquad (2.3)$$

where A = area (m^2); R = resolution (bin/box size, m^2); and M = method (categorical variable where M = underwater video or aerial photography). If the interaction terms $\log(R)*M$ and/or $[\log(R)]^2*M$ were significant, it was not possible to scale from area data collected from transect lines to area data collected from aerial photographs. I used a similar model to determine if it was possible to scale perimeter measurements from transect line data to aerial photograph data:

$$\log(P) = \log(R) + [\log(R)]^2 + M + \log(R)*M + [\log(R)]^2*M \qquad (2.4)$$

where P = perimeter (m); R = resolution (bin/box size, m); and M = method. Once again, if $\log(R)*M$ and/or $[\log(R)]^2*M$ were significant, it was not possible to scale from perimeter data collected from transect lines to perimeter data collected from aerial photographs.

All analyses were performed using SAS (1988). All models were based on a general linear model with a normal error structure. Tolerance of type I error was $\alpha = 0.05$. Residuals were examined for homogeneity, normality and independence.

2.3 Results

2.3.1 Test for lateral heterogeneity across transects

Three sites (Big Brook, Mistaken Cove, and White Rock) did not exhibit lateral heterogeneity for area measurements across transect lines (Table 2.1). Log(A)-log(R) regression line slopes for three transect lines were not significantly different (see Figure 2.4 and Appendix 2 for example). For the other three sites, log(R)*L and/or $[\log(R)]^2$*L were significant indicating that eelgrass spatial configurations vary across transects.

For perimeter measurements, 3 sites (Big Brook, Minchins Cove, and South Broad Cove) did not exhibit lateral heterogeneity, while the other 3 sites did (Table 2.2). Regressing log(P) against log(R) and $[\log(R)]^2$ resulted in parallel slopes at sites without lateral heterogeneity (Figure 2.5). However, only data from 2 lines was used for South Broad Cove because eelgrass was not found on the third line.

2.3.2 Computing between scales

Scaling up eelgrass area measurements from transect lines to aerial photographs was possible at the three sites that did not exhibit lateral heterogeneity (Table 2.3). Interaction terms log(R)*M and $[\log(R)]^2$*M were not significant indicating that regression line slopes for both methods were parallel (Figure 2.6). For these sites, it was possible to measure eelgrass area at a resolution of 0.1 m^2 and scale up to a resolution of 100 m^2 for Big Brook and for Mistaken Cove, and 36 m^2 for White Rock. For all other

Table 2.1 Results testing for lateral heterogeneity of eelgrass area measurements collected in 1999 across three transect lines at 6 sites in Newman Sound showing p-value and β for each variable.

Site	Resolution range†	N	Intercept β_0	log(R) β (p)	$[\log(R)]^2$ β (p)	L† β (p)	log(R)*L† β (p)	$[\log(R)]^2$*L† β (p)
BB	$0.1m^2$ - $15m^2$ $0.1m^2$ - $2m^2$ $0.1m^2$ - $2m^2$	18	1.782	0.02168 (0.0003)	N/A (NS)	-0.1402, -0.03814, 0.0000 (<0.0001)	N/A (NS)	N/A (NS)
HC		30	1.758	0.02518 (<0.0001)	N/A (NS)	-0.2655, 0.01173, 0.0000 (<0.0001)	0.09190, -0.007327, 0.0000 (<0.0001)	0.03332, -0.008084, -0.007406 (0.0101)
MC		19	1.686	0.1342 (<0.0001)	N/A (NS)	0.04929, -0.02107, 0.0000 (<0.0001)	-0.07044, -0.02580, 0.0000 (<0.0001)	N/A (NS)
MI	$0.1m^2$ - $60m^2$ $0.1m^2$ - $60m^2$ $0.1m^2$ - $60m^2$	30	1.747	0.05043 (<0.0001)	-0.01855 (<0.0001)	N/A (NS)	N/A (NS)	N/A (NS)
SB*		14	1.416	0.2359 (<0.0001)	0.04534 (0.0155)	0.1127, 0.0000 (<0.0001)	-0.04734, 0.0000 (0.0255)	N/A (NS)
WR	$0.1m^2$ - $60m^2$ $0.1m^2$ - $60m^2$ $0.1m^2$ - $60m^2$	30	1.746	0.05552 (<0.0001)	-0.002165 (<0.0001)	N/A (NS)	N/A (NS)	N/A (NS)

BB = Big Brook, HC = Heffern's Cove, MC = Minchin's Cove, MI = Mistaken Cove, SB = South Broad Cove, WR = White Rock
N = number of observations; R = resolution; L = line; NS = not significant

† Resolution range, β_L, $\beta_{\log(R)*L}$, and $\beta_{[\log(R)]^2*L}$ listed in following order: left line, middle line, right line.
*Data from two transect lines used.

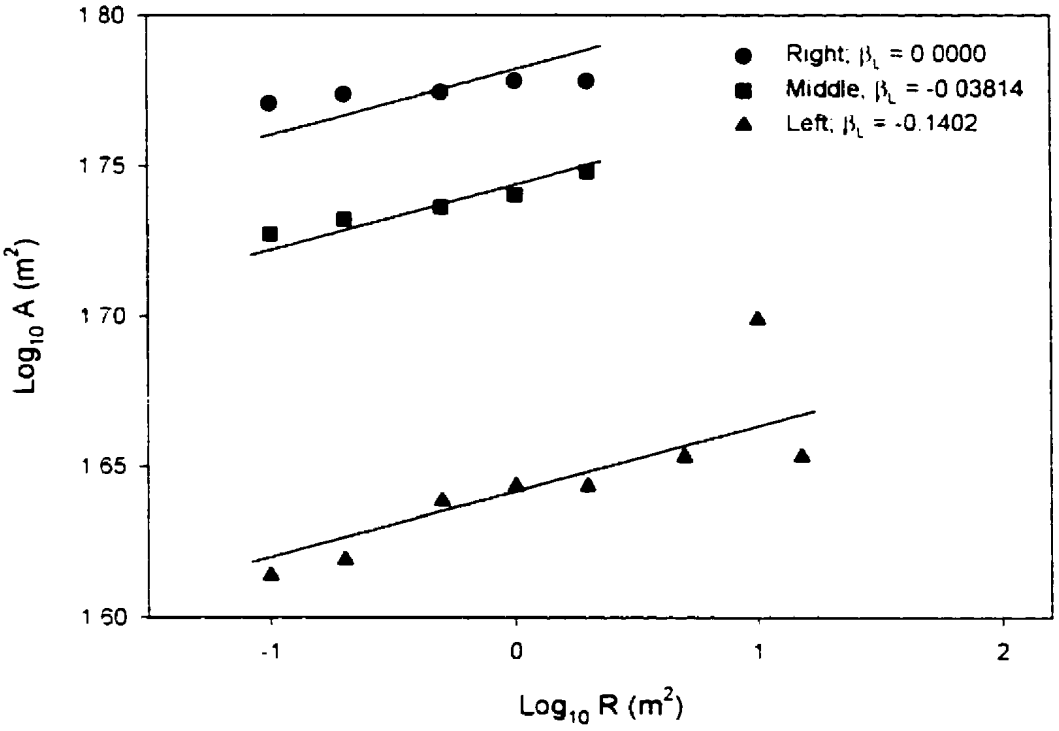

Figure 2.4: Log-log plot of area data for eelgrass habitat along 3 transect lines (labeled right, middle and left, when looking offshore) from Big Brook.
Formula: $\log_{10}A = 1.782 + 0.02168*\log_{10}(R) + \beta_L$.

Table 2.2: Results testing for lateral heterogeneity of eelgrass perimeter measurements collected in 1999 across three transect lines at 6 sites in Newman Sound showing p-value and β for each variable.

Site	Resolution range†	N	Intercept β_0	log(R) β (p)	$[\log(R)]^2$ β (p)	L† β (p)	log(R)*L† β (p)	$[\log(R)]^2$*L† β (p)
BB	0.32m 3.2m 0.32m 7.7m 0.32m 3.9m	25	0.867	0.2869 (<0.0001)	-0.4832 (<0.0001)	0.2731, 0.06348, 0.0000 (<0.0001)	N/A (NS)	N/A (NS)
HC		30	1.167	0.4599 (<0.0001)	-0.8314 (<0.0001)	0.01126, -0.09824, 0.0000 (0.0002)	-0.1553, -0.1459, 0.0000 (0.0102)	0.1286, 0.2784, 0.0000 (0.0260)
MC	0.45m 7.7m 0.45m 7.7m 1m 3.9m	25	1.455	N/A (NS)	-0.6846 (<0.0001)	-0.04018, -0.09152, 0.0000 (0.0007)	N/A (NS)	N/A (NS)
MI		30	1.234	0.3367 (<0.0001)	-0.9014 (<0.0001)	-0.07827, 0.06309, 0.0000 (<0.0001)	0.2100, 0.02348, 0.0000 (<0.0001)	N/A (NS)
SB*	0.32m - 7.7m 0.32m - 7.7m	20	1.318	0.1138 (<0.0001)	-0.7232 (<0.0001)	0.05475, 0.0000 (0.0008)	N/A (NS)	N/A (NS)
WR		29	1.469	0.1155 (<0.0001)	-0.9109 (<0.0001)	-0.1368, -0.1305, 0.0000 (<0.0001)	0.1723, 0.1710, 0.0000 (<0.0001)	N/A (NS)

BB = Big Brook, HC = Heffern's Cove, MC = Minchin's Cove, MI = Mistaken Cove, SB = South Broad Cove, WR = White Rock
N = number of observations; R = resolution; L = line; NS = not significant

† Resolution range, β_L, $\beta_{\log(R)*L}$, and $\beta_{[\log(R)]^2*L}$ listed in following order: left line, middle line, right line.
*Data from two transect lines used.

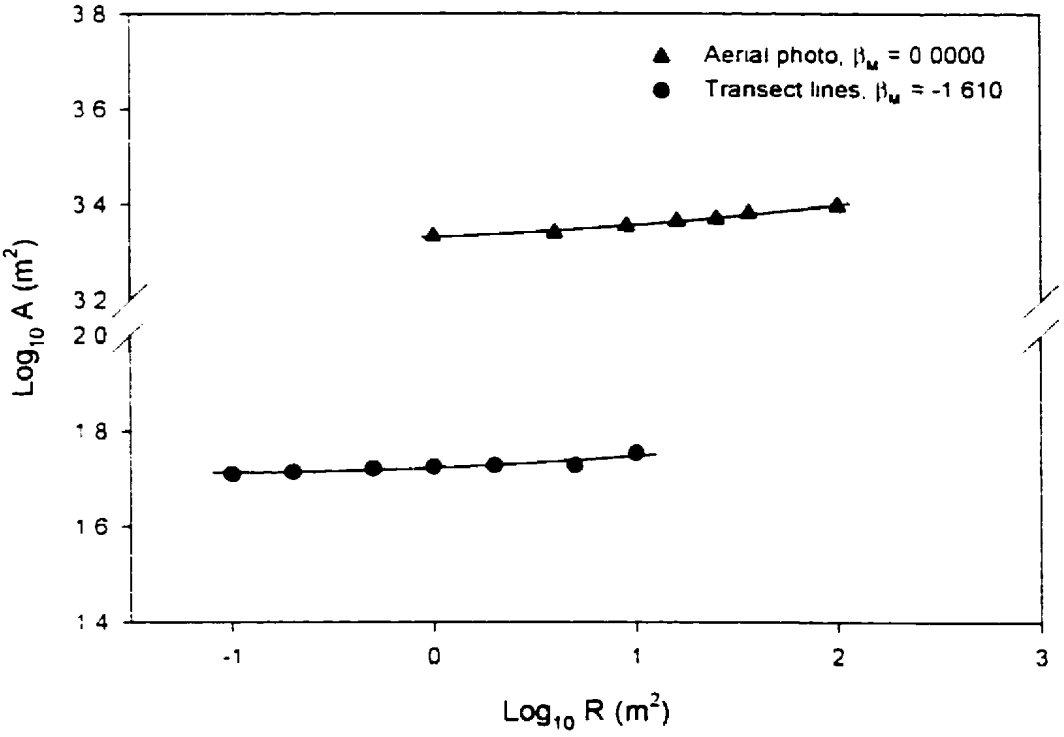

Figure 2.5: Log-log plot of perimeter data for eelgrass habitat along 3 transect lines (averaged) and aerial photo from Big Brook.
Formula: $\log_{10}A = 3.332 + 0.01768*\log_{10}(R) + 0.008098*[\log_{10}(R)]2 + \beta_M$.

Table 2.3: Results for comparison of eelgrass area measurements computed from underwater transects (collected in 1999) and aerial photographs (collected in 2000) for 6 sites in Newman Sound showing p-value and β for each variable.

Site	Resolution range†	N	Intercept β_0	log(R) β (p)	$[\log(R)]^2$ β (p)	M† β (p)	log(R)*M† β (p)	$[\log(R)]^2$*M† β (p)
BB	$0.1m^2$ - $10m^2$ $1m^2$ - $100m^2$	14	3.332	0.01768 (<0.0001)	0.008098 (0.0008)	-1.610, 0.0000 (<0.0001)	N/A (NS)	N/A (NS)
HC		19	3.353	0.01665 (<0.0001)	0.007205 (0.0117)	-1.664, 0.0000 (<0.0001)	0.02570, 0.0000 (0.0011)	N/A (NS)
MC		18	3.486	-0.006321 (<0.0001)	N/A (NS)	-1.782, 0.0000 (<0.0001)	0.09640, 0.0000 (<0.0001)	-0.02543, 0.01565 (<0.0001)
MI	$0.1m^2$ - $5m^2$ $1m^2$ - $100m^2$	13	3.406	0.04762 (<0.0001)	N/A (NS)	-1.666, 0.0000 (<0.0001)	N/A (NS)	N/A (NS)
SB		20	3.193	0.1187 (<0.0001)	N/A (NS)	0.0000, -1.877 (<0.0001)	0.0000, 0.06936 (<0.0001)	N/A (NS)
WR	$0.1m^2$ - $5m^2$ $1m^2$ - $36m^2$	12	3.446	0.06230 (<0.0001)	-0.01054 (0.0028)	-1.702, 0.0000 (<0.0001)	N/A (NS)	N/A (NS)

BB = Big Brook, HC = Heffern's Cove, MC = Minchin's Cove, MI = Mistaken Cove, SB = South Broad Cove, WR = White Rock
N = number of observations; R = resolution; M = method; NS = not significant

† Resolution range, β_M, $\beta_{\log(R)*M}$ and $\beta_{[\log(R)]^2*M}$ listed in following order: underwater transect lines, aerial photograph

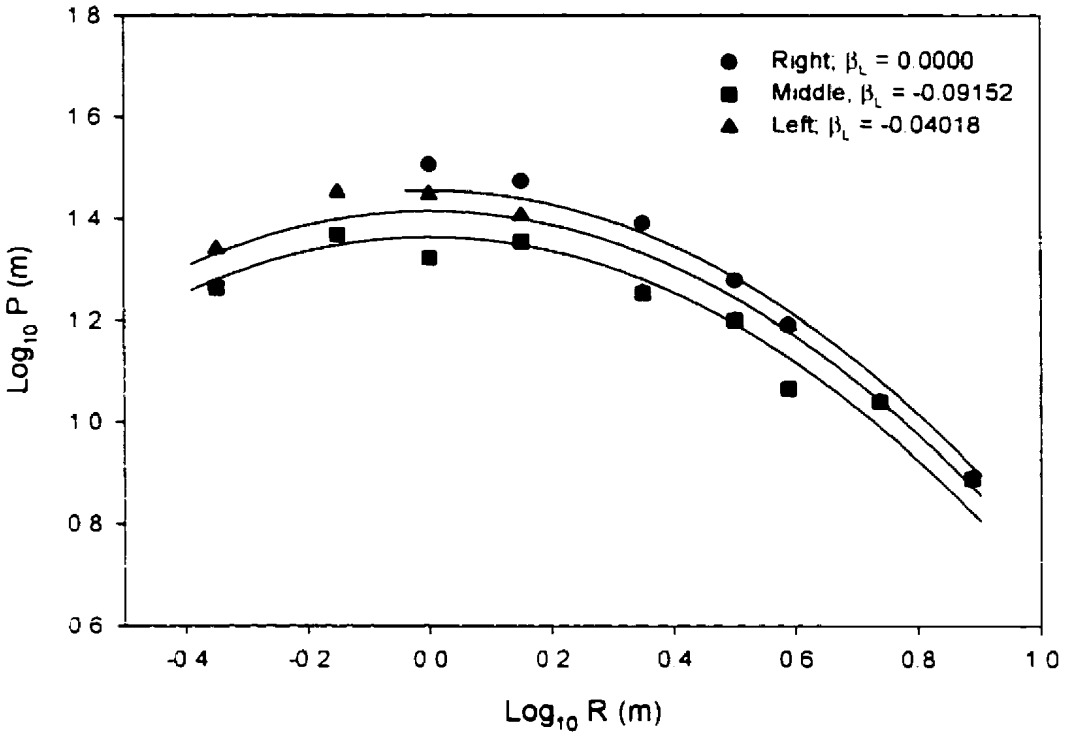

Figure 2.6: Log-log plot of perimeter data for eelgrass habitat along 3 transect lines (labeled right, middle and left when looking offshore) from Minchins Cove. Formula: $\log_{10}P = 1.455 - 0.6846*[\log_{10}(R)]2 + \beta_L$.

sites, the interaction terms log(R)*L and/or $[\log(R)]^2$*L were significant, indicating that scaling exponents computed at the level of transect lines were not comparable to scaling exponents computed from aerial photographs.

Scaling eelgrass habitat perimeter measurements from transect line data to aerial photograph data was possible at the three sites that did not exhibit lateral heterogeneity for perimeter measurements (Table 2.4). This is evident from parallel slopes when log(P) is regressed against log(R) and $[\log(R)]^2$ for both methods (Appendix 3). At Big Brook, it is possible to measure eelgrass area at a resolution of 1 m using data from transect lines or aerial photography and scale up to a resolution of 60 m, and vice versa. At Minchins Cove (Figure 2.7, Appendix 3), the scaling region for perimeter measurements is 1 m to 30 m using either method. Finally, at South Broad Cove, perimeter measurements can be scaled between resolutions ranging from 1 m to 7.7 m. For the other three sites, log(R)*L and/or $[\log(R)]^2$*L were significant, indicating that scaling exponents computed from transect line perimeter data were different from scaling exponents computed from aerial photograph perimeter data.

2.4 Discussion

Seagrass habitat structure is known to vary spatially (Robbins and Bell 1994; Irlandi et al. 1995; Turner et al. 1999) and temporally (Olesen and Sand-Jensen 1994). The measurement of spatial pattern and heterogeneity is dependent upon the scale at which measurements are made (Turner 1989). In this study, I determined that it is possible to scale between large and small scale measurements if the small scale

Table 2.4: Results for comparison of eelgrass perimeter measurements computed from underwater transects (collected in 1999) and aerial photographs (collected in 2000) for 6 sites in Newman Sound showing p-value and β for each variable.

Site	Resolution range†	N	Intercept βo	log(R) β (p)	$[\log(R)]^2$ β (p)	M† β (p)	Log(R)*M† β (p)	$[\log(R)]^2$*M† β (p)
BB	1m - 7.7m 1m - 60m	18	2.194	N/A (NS)	-0.1056 (<0.0001)	-1.184, 0.0000 (<0.0001)	N/A (NS)	N/A (NS)
HC		13	3.027	-0.1676 (0.0285)	-0.4744 (<0.0001)	-1.906, 0.0000 (<0.0001)	0.6553, 0.0000 (0.0008)	-0.3579, 0.0000 (0.0349)
MC	1.4m - 7.7m 1m - 30m	16	3.176	-0.3976 (<0.0001)	-0.2382 (<0.0001)	-1.710, 0.0000 (<0.0001)	N/A (NS)	N/A (NS)
MI		15	2.812	N/A (NS)	-0.3528 (<0.0001)	-1.456, 0.0000 (<0.0001)	N/A (NS)	-0.2318, 0.0000 (0.0238)
SB	2.2m - 7.7m 1m - 5m	10	2.942	N/A (NS)	-0.6016 (<0.0001)	0.0000, -1.755 (<0.0001)	N/A (NS)	N/A (NS)
WR		16	3.120	-0.3951 (<0.0001)	-0.2063 (<0.0001)	-1.6969, 0.0000 (<0.0001)	0.3806, 0.0000 (0.0002)	-0.4583, 0.0000 (<0.0001)

BB = Big Brook, HC = Heffern's Cove, MC = Minchin's Cove, MI = Mistaken Cove, SB = South Broad Cove, WR = White Rock
N = number of observations; R = resolution; M = method; NS = not significant

† Resolution range, β_M, $\beta_{\log(R)*M}$, and $\beta_{[\log(R)]^2*M}$ listed in following order: underwater transect lines, aerial photograph

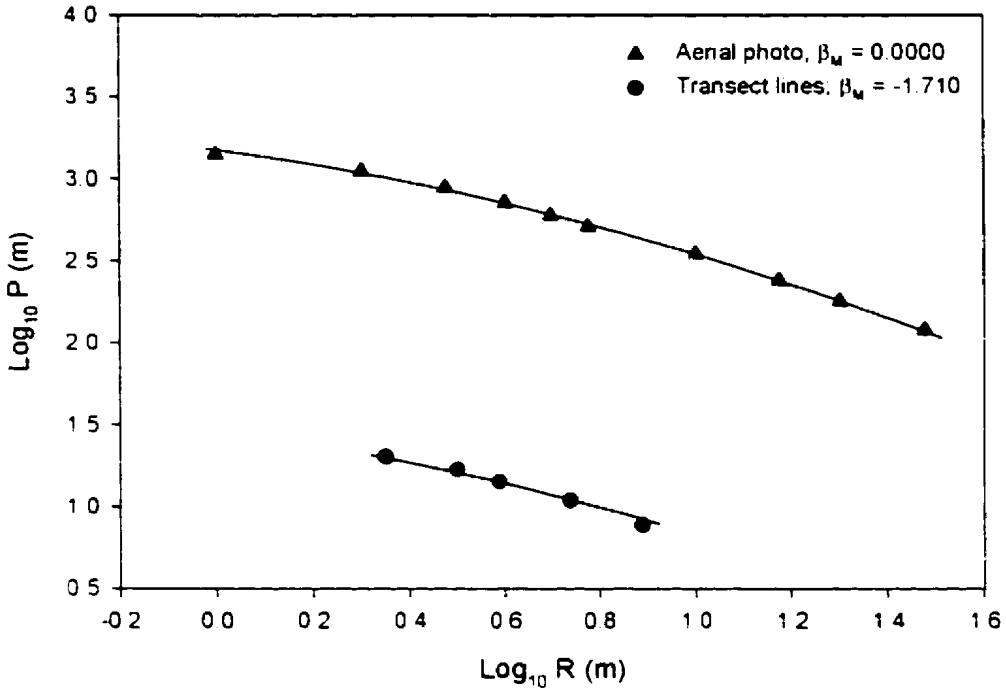

Figure 2.7: Log-log plot of perimeter data for eelgrass habitat along 3 transect lines (averaged) and aerial photo from Minchins Cove.
Formula: $\log_{10}P = 3.176 - 0.3976*\log_{10}(R) - 0.2382*[\log_{10}(R)]2 + \beta_M$.

are homogeneous and can be averaged. First, I compared measurements of eelgrass area and perimeter made at several scales across 3 transect lines within 8 m of each other at 6 sites. I found that 50% of sites exhibited lateral heterogeneity for both area and perimeter measurements. In other words, scaling exponents computed for each transect line were significantly different from each other. This supports the idea that eelgrass habitat varies with respect to scale and location.

Several factors affect why only some sites exhibit lateral heterogeneity, including depth, modification of normal temperature and salinity regimes (Thayer et al. 1984), and level of exposure or wind and current. Light availability appears to be the primary factor limiting both depth and up-estuary penetration of eelgrass within its temperature and salinity ranges (Thayer et al. 1984). *Z. marina* has relatively narrow temperature requirements (Setchell 1929) but it is considered euryhaline (Rasmussen 1977). However, variation in eelgrass habitat between sites cannot be attributed to salinity and temperature because these factors do not differ significantly among sites in Newman Sound (Gotceitas et al. 1996). In shallow water, waves reshape eelgrass meadows. At all depths, currents erode sediments, matured plants, and seeds, and prevent deposition of material (Thayer et al. 1984). Ings et al. (in prep) found that eelgrass abundance was positively correlated with coastline complexity, which can be an indicator of level of exposure. I suggest exploring the possibility that eelgrass complexity may also be related to coastline complexity.

The fact that scaling exponents differed between transect lines was predictable at some sites based on visual observation. Eelgrass at Big Brook forms a meadow with very

few open areas of bare substrate within the eelgrass beds (see Appendix 1). This distribution accounts for the lack of lateral heterogeneity in area and perimeter scaling exponents at this site. South Broad Cove eelgrass is at the other end of the continuum with distinct patches growing in areas of bare substrate (see Appendix 1). All other sites fall between these two extremes, generally resembling meadows with "holes" or bare areas of non-vegetated substrates (e.g., mud, sand, silt, cobble, etc.), therefore making it difficult to predict if scaling exponents would be similar for all three transect lines at these sites.

From the second analysis, I determined that it is sometimes possible to scale between large-scale measurements and small-scale measurements. Measurements of eelgrass area and perimeter taken at the resolution of an aerial photograph were extrapolated to the resolution of a transect line for three sites. Common scaling exponents were computed for these sites using two different methods which varied in resolution by up to 4 orders of magnitude. Therefore, it is possible to quantify eelgrass habitat characteristics at large scales and compute to smaller scales - and vice versa - using a common scaling law. This function can be applied to new data sets within the scaling region because scaling exponents were constant for both methods.

Scaling from 1 m wide transect lines to 60 m wide aerial photographs is not possible when eelgrass habitat is not laterally homogeneous, as found at some sites. However, when all three transect lines exhibit similar scaling exponents, the average of eelgrass measurements resemble eelgrass measurements at the scale of an aerial photograph. Therefore, the problem lies not in scaling from small resolutions to large

resolutions, or vice versa, but in having too few transect lines to accurately represent the aerial photograph. If the precise location of the transect lines could be extracted from the aerial photographs, the problem of lateral heterogeneity may not be an issue. A direct comparison of the same strip of eelgrass could be made using either method.

Both methods of eelgrass habitat measurement are valuable, depending on which range of resolutions one is interested in. Underwater transect line video provides detail which cannot be captured in an aerial photograph. However, aerial photographs are easier and cheaper to obtain, and provide a broader view of spatial patterns of eelgrass bed growth. Thus, if one had to choose, it would be sufficient to use the cheapest method when measuring eelgrass spatial patterns, knowing that a scaling exponent can be used to compute measurements at smaller or larger scales.

Parameters and processes important at one scale are frequently not important or predictive at another scale, and information is lost as spatial data are considered at coarser scales of resolution (Schneider and Piatt 1986; Turner 1990). This rate of loss of information with resolution is a key piece of information that can be quantified with scaling laws. Ecological problems often require the extrapolation of fine-scale measurement for the analysis of broader-scale phenomena. Therefore the development of methods that will allow computation across scales has become a critical task (Turner 1990). I have shown that it is possible to conduct multi-scale studies of eelgrass habitat and compute common scaling laws of habitat measurements using different methods. These multi-scale analyses can be applied elsewhere in ecological studies to clarify issues

such as relationships between species abundance and habitat, which may occur at several scales.

2.5 Acknowledgements

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Chapter 3: Influence of the spatial complexity of eelgrass (*Zostera marina*) on age 0 Atlantic cod (*Gadus morhua*) densities

3.1 Introduction

Multi-scale spatial analyses have become progressively more prevalent in ecological studies (Schneider 2001). Investigators have become increasingly aware that the scale at which their study is designed can have a drastic impact on the results they will obtain (Dayton and Tegner 1984). Multi-scale studies to date have focused mainly on terrestrial systems. However, studies in aquatic systems are becoming more common (e.g., Robbins and Bell 1994; Turner et al. 1999). Ecologists are aware that aspects of aquatic habitats such as amount of available habitat (Adams 1976; Orth and Heck 1980), and size or shape of patches (Hamazaki 1996) influence the distribution and behavior of organisms. Contemporary research has focused on the influence of configuration or complexity of habitat on organisms and ecological processes (Gotceitas and Colgan 1989; Irlandi et al. 1995; Irlandi 1997; Graham et al. 1998; Hokit et al. 1999). However, complexity patterns found at small spatial scales may be very different from those found at broader spatial scales (Wiens 1989). Thus, studies identifying scale-dependent relationships between organisms and habitat are becoming more prevalent (Otto 1996; Azovskii and Chertoprud 1997; Ritchie 1998; Snover and Commito 1998).

Fractal geometry has been a useful tool in ecological sciences for quantifying aspects of habitat over a range of spatial scales (Sugihara and May 1990; Hastings and Sugihara 1993; Johnson et al. 1995; Kenkel and Walker 1996). Fractals provide a

numerical expression of complexity which is independent of the nature of habitat and are related to the scale at which the habitat is viewed (Gee and Warwick 1994). This type of analysis has been used to determine spatial patterns in landscapes (Krummel 1987; Otto 1996; Ritchie 1998; Nikora 1999), ecological habitats (Williamson and Lawton 1991), and vegetation (Morse et al. 1985; Palmer 1988; Scheuring and Riedi 1994; van Hees 1994). The majority of these fractal-based studies focus on terrestrial systems. However, fractal analyses are becoming common in aquatic systems as well (Gee and Warwick 1994; Simon and Simon 1995; Azovskii and Chertoprud 1997; Snover and Commito 1998; Turner et al. 1999).

Seagrasses grow in complex structural arrangements in marine environments. They exhibit hierarchical arrangements of spatial structure, ranging from individual rhizomes and shoot groups (centimeters to meters), to discrete patches of seagrass (meters to tens of meters), to seagrass meadows (tens of meters to kilometers) (Robbins and Bell 1994; Turner et al. 1999). Seagrass meadows may be extensive and continuous or highly fragmented and arranged into a mosaic of small patches (Robbins and Bell 1994). Several investigators have measured components of seagrass habitat, including patch size (Irlandi 1997), shoot density (Bell and Westoby 1986; Graham et al. 1998), biomass (Adams 1976), and leaf height (Bell and Westoby 1986). Complexity of seagrass habitat based on spatial patterning has rarely been quantified (but see Turner et al. 1999 and O 2002). Investigators have often referred to certain aspects of seagrasses as measures of complexity, but often provide some measure of biomass, such as leaf height or density (Bell and Westoby 1986; Graham et al. 1998), and do not provide a

quantitative measurement of habitat structural complexity. When measurements of spatial patterning of habitat structure have been made, they have been measured at only one scale (Irlandi et al. 1995). Techniques developed for terrestrial landscapes, such as fractal analyses, can be applied to measure the complex spatial patterning of seagrasses at several resolutions.

Organism density and diversity are often related to characteristics of seagrass habitat. Orth et al. (1984) summarize studies that describe the influence of seagrass plant architecture on the associated animal distribution and abundance. Orth and Heck (1980) found that fish abundance and species number were influenced by water temperature and eelgrass biomass. Orth et al. (1984) proposed that the abundance of many species, both epifauna and infauna, is positively correlated with two aspects of plant morphology: 1) the root-rhizome mat, and 2) the plant canopy. When they manipulated seagrass height and density, Bell and Westoby (1986) observed ambiguous effects on fish and decapod abundance and species richness. They found that the abundance of some species increased, while others decreased in response to manipulations. Bell and Westoby (1986) concluded that a model predicting responses of species richness and abundance to changes in physical complexity of seagrasses existing at the time could not be supported. Graham et al. (1998) found a decreasing exponential relationship between feeding efficiency of mummichogs and eelgrass shoot density. Overall, it has become clear that seagrass structural patterns have a major effect on the organisms associated with these habitats.

Eelgrass (*Zostera marina*) is an important habitat for juvenile Atlantic cod (*Gadus morhua*) (Tupper and Boutilier 1995; Borg et al. 1997). The structurally complex plant provides refuge from predators (Gotceitas et al. 1997) and provides a habitat for invertebrate prey (Orth et al. 1984), promoting rapid growth of juvenile cod (Tupper and Boutilier 1995). In Newfoundland, studies using scuba have shown that age 0 cod are often found associated with eelgrass, as opposed to other substrates such as mud, sand, gravel or rock (Gotceitas et al. 1997). However, cod densities measured by beach seine at paired eelgrass and non-eelgrass sites were significantly higher at only 2 out of 3 paired sites (Gotceitas et al. 1997). Furthermore, Norris et al. (in prep) found that the number of cod at a given site could not be related to percent cover of eelgrass. Ings et al. (in prep.) found the relationship between cod density and eelgrass cover was inconsistent between sites in certain years, with significant associations in some years but not others.

In this study, I undertook a two-phase analysis to examine the hypothesis that eelgrass structural complexity, rather than just percent cover at a fixed scale, would explain variation in the proportion of seine hauls that catch age 0 cod and in age 0 cod density among eelgrass sites. Specifically, I expected the highest proportion of seine hauls containing cod and the highest densities of cod to be found at intermediate eelgrass complexities. The intermediate optimum hypothesis is based on my belief that low complexity eelgrass habitat has too little edge (possibly leading to decreased access to food) whereas high complexity eelgrass habitat has too much edge (possibly leading to increased risk of predation). I analyzed density of age 0 Atlantic cod at 8 sites in

Newman Sound, Newfoundland in relation to eelgrass complexity. Using measurements of area and perimeter of eelgrass habitat, I determined complexity using fractal analyses.

3.2 Methods

3.2.1 Study area

Newman Sound is a fjord located in southwestern Bonavista Bay, on the northeastern coast of Newfoundland, Canada (Figure 3.1). Eight sites were chosen based on the presence of eelgrass and because preexisting and concurrent juvenile cod data are available from these sites (Gregory et al. 2001, Ings et al. in prep, O 2002). Eelgrass was associated with mud, silt, sand, and gravel substrates and, where present, is generally restricted to depths of less than 6 m in Newman Sound.

3.2.2 Aerial photography

Aerial photographs of the 8 sites were taken in August 2000 (see Appendix 1) from a single-engine Cessna floatplane at altitudes between 150 m and 300 m. Prior to taking photographs, markers were set out at each site to delineate the area sampled by beach seine. This procedure allowed for scaling of images and correction of camera angle for each photograph. Each plywood marker measured 0.6 m x 0.6 m and was spray-painted fluorescent orange. One marker floated on the ocean surface 50 m offshore and was anchored with a rope tied to a concrete block. Two other markers were placed on the

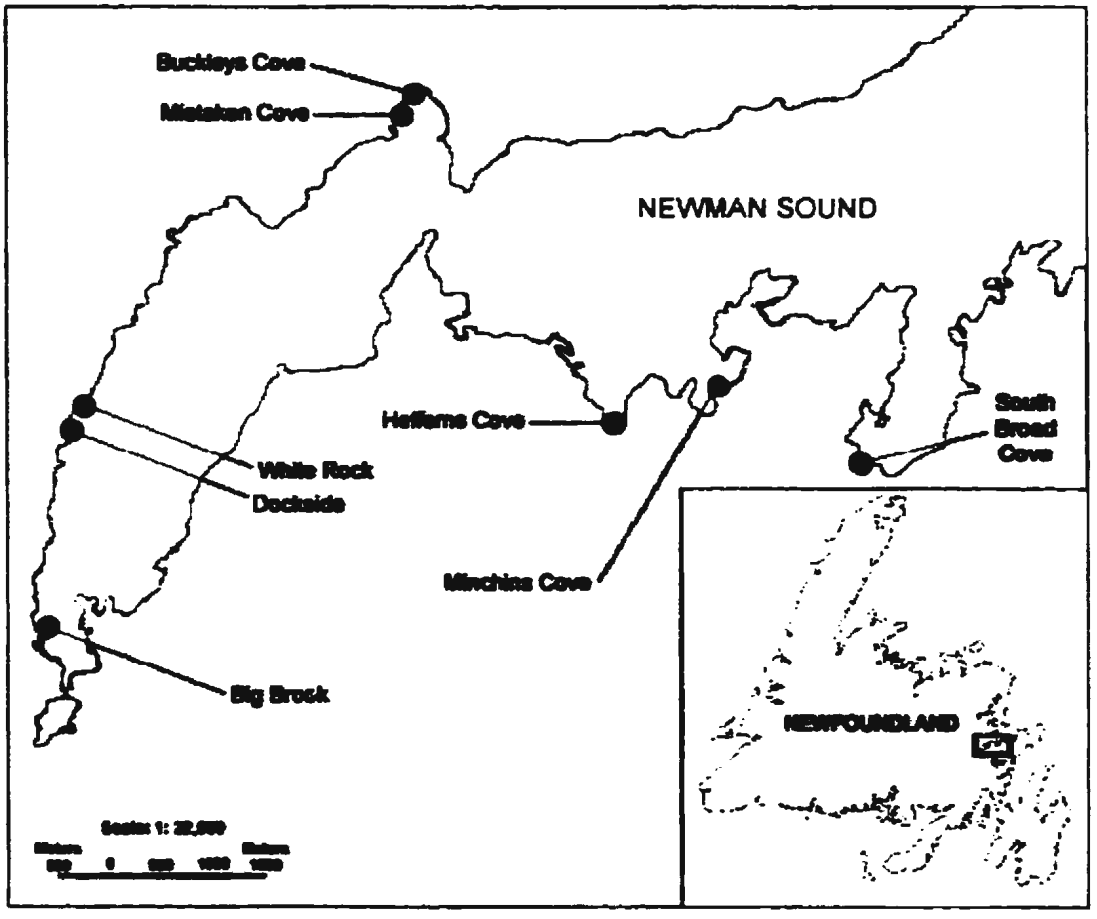

Figure 3.1: Map of the study area, Newman Sound, Newfoundland, showing the location of the 8 sites used in this study: Big Brook, Dockside, White Rock, Buckleys Cove, Mistaken Cove, Hefferns Cove, Minchins Cove, and South Broad Cove.

beach 25 m apart; a compass was used to ensure that the three markers formed a 90 degree angle (Figure 3.2). Flights were performed near midday when surface glare and surface winds were minimal. Pictures were taken with a 35-mm Pentax FX10 camera, fitted with a 28-80 mm Pentax F Zoom lens (set to 50 mm), haze filter, and polarizer filter. Pictures were taken as close as possible to directly vertical over the site to avoid glare.

3.2.2.1 Image editing

Aerial photographs were developed to a Kodak Digital Science Photo CD Master disc, with the highest resolution level being 2048 x 3072 pixels. Images were edited using Adobe Photoshop 5.5. Each image was cropped to represent 3600 m^2 on the ground and adjusted to the correct angle and scale using transformation features (skewing and scaling) in Adobe Photoshop.

3.2.3 Measuring habitat complexity

3.2.3.1 Ground truthing

Before quantifying habitat from the aerial photographs, each site was ground surveyed using an aquascope (PVC with Plexiglas bottom). A rough map of each site was drawn with a general layout of habitat types (e.g., eelgrass, *Fucus*, mineral substrates), enabling me to verify the habitat types observed on aerial photographs.

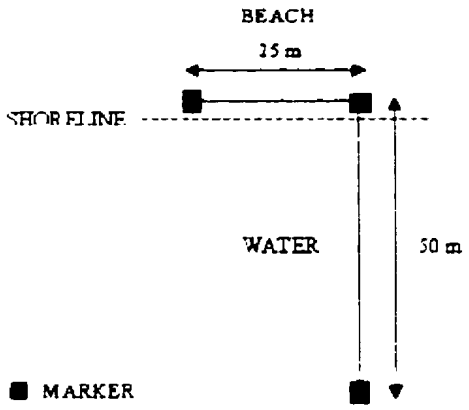

Figure 3.2: A depiction of the layout of markers at each site for purposes of scaling aerial photographs correctly. Onshore markers were 25 meters apart. The third marker was 50 meters offshore. All three markers formed a 90° angle.

3.2.3.2 Box counting

I used a box-counting method (Sugihara and May 1990) to quantify eelgrass habitat dimensions (area and perimeter) at several scales of resolution from the aerial photographs. A grid containing 3600 boxes (1 m^2 each on the ground) was placed over each digital aerial photograph. Two types of data from the image were transferred manually to printed hard copy replicas of the grid: presence or absence of: (1) eelgrass habitat (area measurement) and (2) eelgrass habitat edge (perimeter measurement). Once area and perimeter data from the highest resolution grid were transferred, grids of lower resolution (i.e., fewer boxes) were placed over the 3600-box grid. The number of boxes containing area and perimeter were counted at resolutions of 1 m^2, 4 m^2, 9 m^2, 16 m^2, 25 m^2, 36 m^2, 100 m^2, 225 m^2 and 400 m^2. Eelgrass habitat area was calculated by multiplying the number of boxes that contained eelgrass at a given resolution by the size (m^2) of the boxes. Eelgrass habitat perimeter was calculated by multiplying the number of boxes that contained perimeter at a given resolution by the length of a side (m) of a box.

3.2.3.3 Fractal analysis of eelgrass habitat

Area and perimeter of eelgrass habitat were used to calculate a fractal dimension [$\log(A) \sim (D_f)\log(P)$: where A = the area of a 2-dimensional section of habitat; P = the perimeter of habitat at a particular length-scale; D_f = the fractal dimension (Turner 1989)], which has been frequently used as an index of complexity in landscape and habitat studies (Lovejoy 1982, Turner 1989, Turner et al. 1999). Residuals were checked for homogeneity, normality and independence, and the scaling region (linear portion) of

the line was chosen to extract D_f. D_f is computed by subtracting the slope of the regression line from 1.

3.2.4 Historical cod catch data: beach seining

Cod density data were collected bi-weekly by beach seine in 1998, 1999 and 2000 at 8 sites from mid-July to mid-November. Fish samples were collected using a 25 m beach seine (wings and belly 19 mm stretch mesh, codend 9 mm stretch mesh bag; 24.4 m headrope, 26.2 m footrope; aluminum spreader bars on each wing were 75 cm long and 25 mm in diameter). The net was deployed from a 6 m boat at a distance of 55 m offshore, and then retrieved by two individuals standing 16 m apart on the shore. The seine was pulled along the bottom and sampled the lowest 2 m of the water column and approximately 880 m^2 of the bottom. For additional details on deployment and retrieval of the seine, see Schneider et al. (1997). Scuba observations have shown that approximately 95% of the fish in the path of beach seine nets are captured (Gotceitas et al. 1996). All fish collected were identified to species and counted. Juvenile cod were aged by applying previously established age-length relationships for juvenile Atlantic cod in Newfoundland waters (age 0: ≤ 10 cm SL (standard length), age 1: 10 to 20 cm SL, age 2: 20 to 30 cm SL, and age 3 and older: > 30 cm SL) (Gregory et al. 2000). All fish were released after sorting. Mortality due to sampling and handling was negligible (pers. obs.). Cod density data from 1999 and 2000 were not used for two sites (Dockside and Buckleys Cove) due to a concurrent manipulation experiment at these sites (Laurel et al. in prep).

3.2.5 Relating cod density and habitat complexity

I conducted my analysis of the relationship between age 0 cod and eelgrass complexity in two phases: Phase I, presence of age 0 cod versus eelgrass complexity; Phase II, density of age 0 cod, if present, versus eelgrass complexity. For Phase I, I computed the proportion of seine hauls that contained age 0 cod for each site for each month (all years combined) and for each year (all months combined). I regressed proportion of successful seine hauls against D_f for each site, using a binomial error distribution with a logit link (most commonly used with binomial error) (McCullagh and Nelder 1989).

In Phase II, I investigated the relationship between habitat complexity and age 0 cod density by regressing fish density against D_f for each site. Analyses were done separately by month for July – November in all years (1998-2000), and for each month within each year based on a biological model with an intermediate optimum hypothesis. I chose a gamma error structure with a log link (McCullagh and Nelder 1989).

All analyses were performed using SAS (1988). Tolerance of type I error was $\alpha = 0.05$. Residuals were examined for homogeneity, normality and independence.

3.3 Results

3.3.1 Fractal analysis of eelgrass habitat

Log-log plots of area versus perimeter (e.g., see plot for Mistaken Cove in Figure 3.3) resulted in a D_f (index of complexity) for each site, ranging from 1.0 to 1.3625

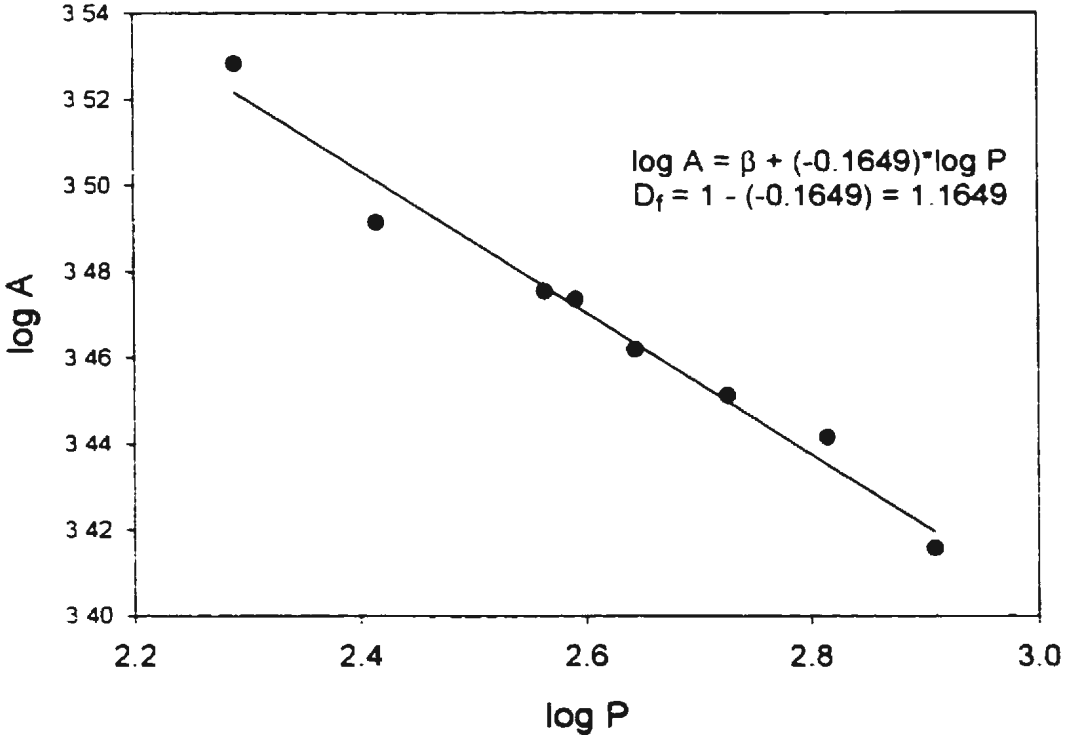

Figure 3.3: Log-log plot of area (A) and perimeter (P) for Mistaken Cove (MI).

(Table 3.1). Sites that were meadow-like had the lowest fractal dimensions (D_f = 1.0 - 1.093). Big Brook differed from other sites as it had a meadow-type arrangement of eelgrass and data did not fit a line. Hence Big Brook eelgrass habitat was considered Euclidean with a D_f of 1.0. A site with highly patchy eelgrass habitat (South Broad Cove) had the highest fractal dimension (D_f = 1.3625). All other sites were in the middle of the meadow-patchy continuum and had intermediate fractal dimensions.

For each site, a scaling region (e.g., Morse et al. 1985; Nikora et al. 1999) was chosen for the regression lines based on an upper limit. When the box size is large in the box-counting method, it is probable that all boxes will contain eelgrass (i.e., area measurements were at a maximum of 3600 m^2). This is an artefact of the method and beyond this upper limit, no new information for habitat could be derived. The upper limit, and thus the scaling region, was different for each site, with the maximum box size ranging from 25 m^2 to 400 m^2 (Table 3.1).

3.3.2 Phase I: Presence of age 0 cod versus eelgrass complexity

When all months were combined, the proportion of successful seine hauls was positively related to eelgrass complexity according to the following equation:

$$P = e^{(-2.32 + 4.54 * D_f + \beta_M * M)} / [1 + e^{(-2.32 + 4.54 * D_f + \beta_M * M)}] \quad (3.1)$$

where P = # seine hauls with age 0 cod/total # seine hauls; D_f = fractal dimension and M = month (see Appendix 4). The interaction between month and fractal dimension was not significant and was removed from the model. Thus, one equation could be used for all 5 months with β_M varying according to month (Figure 3.4). During early months (July and

Table 3.1: Results of complexity analysis showing maximum scale (box size) used and parameter estimates obtained for each site. Regression equation: $\log A = \beta o + \beta_P * \log P$, where A = area and P = perimeter.

Site	Maximum scale (box size m^2)	β_P	Standard error (α)	βo	Standard error (β)	p value
Big Brook	N/A	0	N/A	0	N/A	N/A
Buckley's Cove	36	-0.0754	0.0045	3.7168	0.0128	<0.0001
Dockside	36	-0.0930	0.0055	3.7727	0.0157	<0.0001
Heffern's Cove	400	-0.1013	0.0065	3.6611	0.0172	<0.0001
Minchin's Cove	25	-0.0566	0.0038	3.6635	0.0113	0.0007
Mistaken Cove	225	-0.1649	0.0108	3.8991	0.0283	<0.0001
South Broad Cove	400	-0.3625	0.0249	4.3058	0.0653	<0.0001
White Rock	100	-0.1565	0.0120	3.9413	0.0340	<0.0001

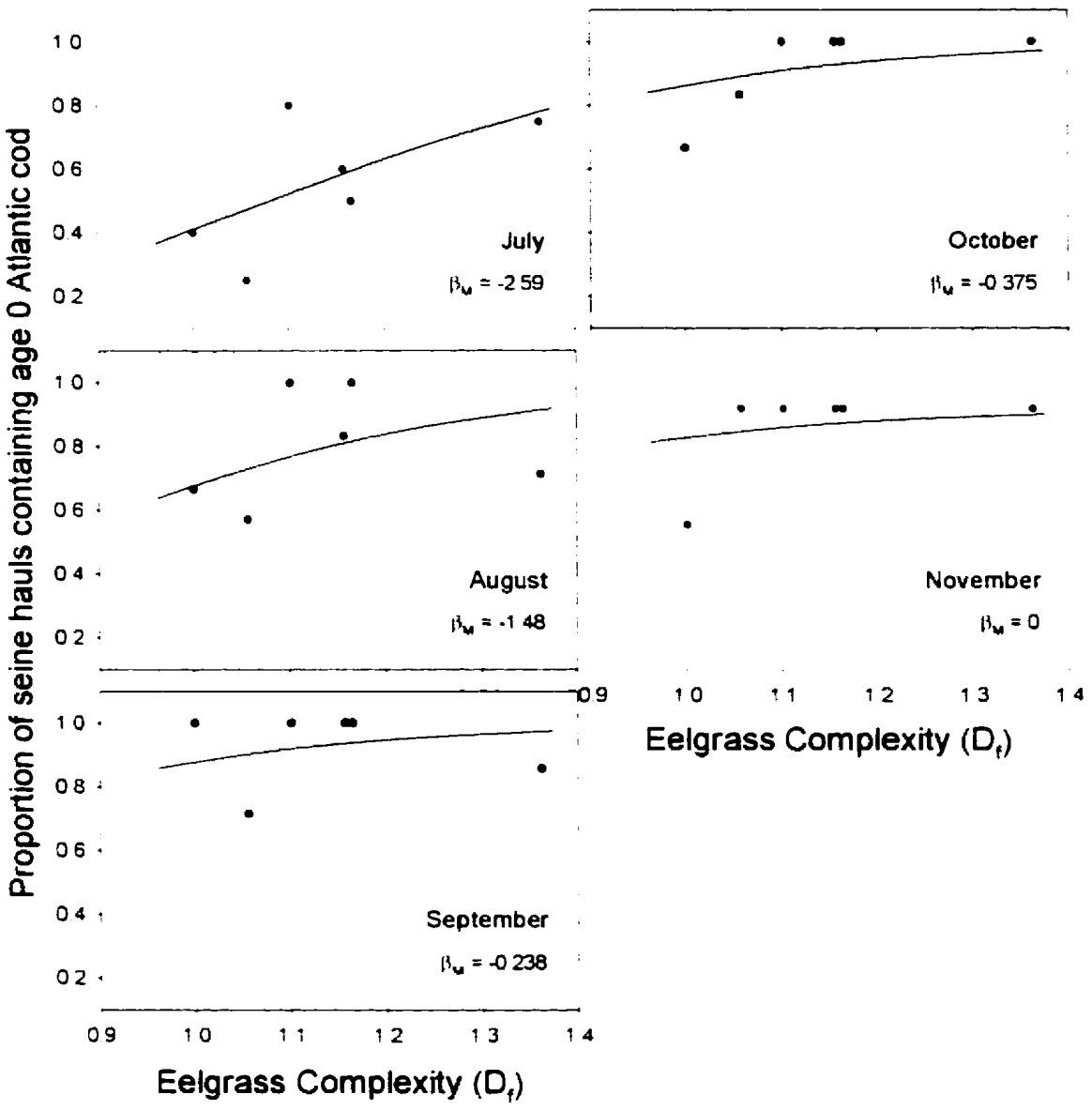

Figure 3.4: Proportion of seine hauls (P) with age 0 Atlantic cod for July, August, September, October, and November, where all years have been combined. Formula: $P = e^{(\beta o + \beta_{D_f} * D_f + \beta_M * M)} / (1 + e^{(\beta o + \beta_{D_f} * D_f + \beta_M * M)})$, where βo = -2.32, β_{D_f} = 4.54, and β_M shown for each month.

August) cod were caught more often at sites of higher eelgrass complexity. Late in the season (September, October, and November), nearly all seine hauls at every site contained age 0 cod.

3.3.3 Phase II: Density of age 0 cod, if present, versus eelgrass complexity

Age 0 cod density data from all years were combined in the following model:

$$C = \beta_0 + \beta_Y \cdot Y + \beta_{D_f} \cdot D_f + \beta_{D_f^2} \cdot D_f^2 + \beta_{Y\,D_f} \cdot Y \cdot D_f + \beta_{Y\,D_f^2} \cdot Y \cdot D_f^2 + \varepsilon \qquad (3.2)$$

where C = cod density (#/seine haul), Y = year, and D_f = fractal dimension of eelgrass. The interaction terms $\beta_{Y\,D_f} \cdot Y \cdot D_f$ and $\beta_{Y\,D_f^2} \cdot Y \cdot D_f^2$ were not significant, nor was $\beta_Y \cdot Y$; all three terms were removed from further analysis. To determine if the interaction between month and D_f was important I applied the following model:

$$C = \beta_0 + \beta_M \cdot M + \beta_{D_f} \cdot D_f + \beta_{D_f^2} \cdot D_f^2 + \beta_{M \cdot D_f} \cdot M \cdot D_f + \beta_{M\,D_f^2} \cdot M \cdot D_f^2 + \varepsilon \qquad (3.3)$$

where C = cod density (#/seine haul), M = month, and D_f = fractal dimension of eelgrass. The interaction terms $\beta_{M \cdot D_f} \cdot M \cdot D_f$ and $\beta_{M \cdot D_f^2} \cdot M \cdot D_f^2$ were not significant. However when I removed one interaction term at a time, all variables became significant. I concluded that interaction was present and so analyzed the data separately for individual months.

The relationship between cod density and eelgrass complexity (D_f) varied with month. The cod density-complexity relationship in September was similar throughout all three years – a quadratic – and supported the intermediate optimum hypothesis (see Figure 3.5 and Appendix 5):

$$C = (e^{-70.502}) \cdot (e^{120.11 \cdot D_f}) \cdot [e^{-47.730 \cdot (D_f^2)}] \qquad (3.4)$$

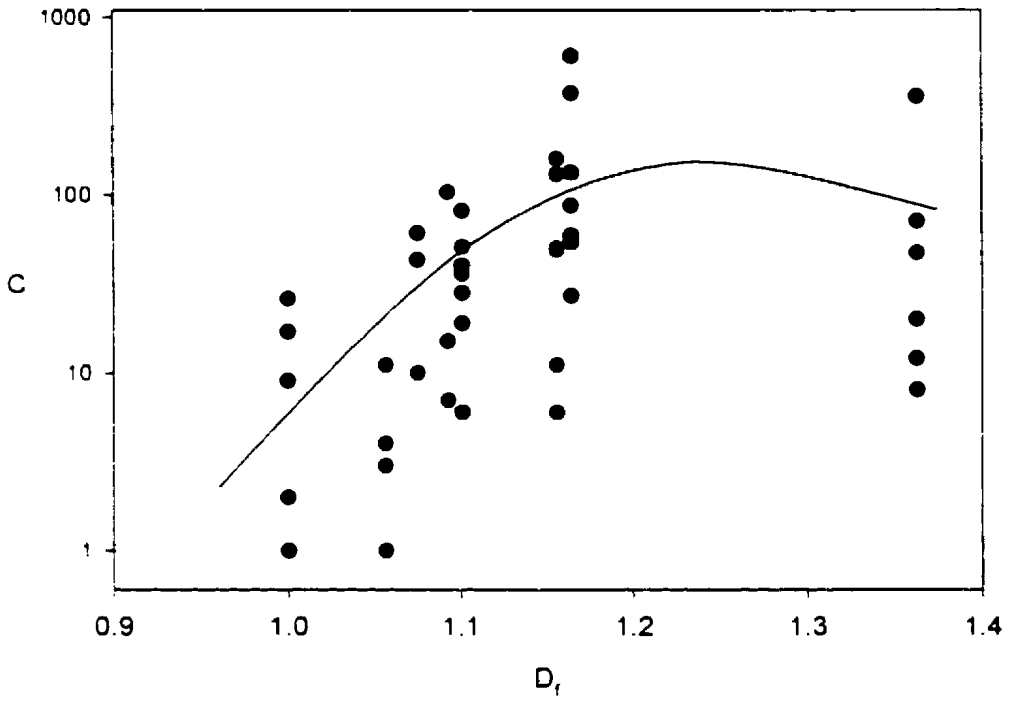

Figure 3.5: Relationship between cod density (C) and eelgrass complexity (D_f) for September, all three years combined.

For all other months difficulties were encountered: (1) residuals were either non-normal; (2) or heterogeneous; or (3) D_f was not significant (Appendix 6). I analyzed each month separately by year, with the exception of September (Appendix 6). Months that had significant results with acceptable residuals are given in Table 3.2. In total, cod densities in four months out of 15 showed a relationship with eelgrass complexity (D_f). These relationships were either linear (August 2000 and November 1999) or quadratic (October 2000 and November 1998).

3.4 Discussion

Eelgrass habitat complexity ranged from $D_f = 1.0$ to 1.36. Sites that were low in complexity resembled a meadow with very little perimeter. At such sites, as resolution decreases, area and perimeter measurements change very little, resulting in a gentle regression line slope and a D_f that is close to 1.0. At sites where eelgrass habitat is slightly patchy, area and perimeter measurements change a lot as resolution decreases. These sites have intermediate values of D_f. Finally, high complexity sites (e.g., South Broad Cove, $D_f = 1.36$) have non-continuous patches of eelgrass. This results in area and perimeter measurements changing quickly as resolution decreases, a steep regression line slope, and a relatively high D_f. Based on personal observation and personal discussion with colleagues, it is believed that the fractal dimension of eelgrass at a given site does not change significantly throughout the season or over years.

Table 3.2: p values and parameter estimates for monthly analyses that had significant results for the relationship between cod density (C) and eelgrass complexity (D_f): $C = (e^{\beta_0}) \cdot (e^{\beta_{D_f} D_f}) \cdot [e^{\beta_{D_f^2} (D_f^2)}] + \varepsilon$ **or** $C = (e^{\beta_0}) \cdot (e^{\beta_{D_f} D_f}) + \varepsilon$

		D_f		D_f^2		Intercept
Month	**Year**	**p value**	β_{D_f}	**p value**	$\beta_{D_f^2}$	β_0
August	1999	0.0006	6.5564	N/A	N/A	-3.1876
October	2000	0.0353	165.46	0.0375	-66.637	-98.677
November	1998	0.0072	90.065	0.0064	-38.087	-51.628
November	1999	0.0429	-11.5234	N/A	N/A	16.3732

There are several factors that may influence growth and thus, complexity of eelgrass habitat. These factors include sediment type (Probert and Benchly 1999), ice scour (Robertson and Mann 1984; Schneider and Mann 1991), light availability (Backman and Barilotti 1976; Dennison and Alberte 1982, 1985, 1986; Orth and Moore 1983, 1988), turbidity (Orth and Moore 1983; Kemp et al 1983; Zimmerman et al 1991; Dennison et al 1993), modification of normal temperature and salinity regimes (Thayer et al. 1984), and level of exposure or wind and currents (Fonseca et al. 1983; Thayer et al. 1984; Wanless et al 1988; Robblee et al 1991). Factors influencing the complexity of eelgrass habitat have not been studied in Newfoundland.

Eelgrass habitat provides a number of nursery-type functions that benefit organisms associated with it (e.g., see Chapter 1). Studies have shown that age 0 Atlantic cod utilize eelgrass habitat (Tupper and Boutilier 1995; Gotceitas et al. 1997). Cod and eelgrass associations have been found using two scales of resolution for eelgrass abundance (Ings et al. in prep.). Cod density increased with eelgrass abundance on a large scale and this relationship was strongest at high densities (Ings et al. in prep.). Knowing that eelgrass measurements change with scale, I applied this information to cod density data with confidence that I had incorporated the scale at which these fish associate with this habitat.

The analysis of age 0 cod abundance was carried out in two phases under the assumption that different processes, and hence a different model, applied to presence of cod versus density of cod if present. The proportion of successful seine hauls at a given site was dependent on eelgrass complexity. A high proportion of seine hauls contained

age 0 cod at higher complexity sites during all months of the year and in all years. Age 0 cod were more likely to be caught at higher complexity sites in early months (July and August). However, later in the season, cod were found equally at all sites. This relationship may be density-dependent because increases in the abundance of age 0 cod in less suitable habitat (non-eelgrass areas) are known to occur when settlement strength is high (Grant and Brown 1998).

Age 0 Atlantic cod appear to move into nearshore habitats in a recruitment pattern consisting of at least two settlement pulses each year – the first arriving in August, the second in late September to October (Beacham et al. 2000, Gregory et al. 2000). By November, water temperatures start to decline and it is thought that juvenile cod begin to move into deeper waters (Methven and Bajdik 1994). During recruitment pulses, it has been suggested that cod settle at all sites and density patterns seen thereafter are a result of differential survival (Tupper and Boutilier 1995). Alternatively, cod density patterns may also be a result of selective recruitment to areas of preferred habitat (Gregory and Anderson 1997). My results suggest a combination of both hypotheses is true. During the August pulse, proportions of seine hauls with age 0 cod are highest at sites with highly complex eelgrass suggesting – in support of the second hypothesis - that one is more likely to catch cod at these sites. However, when cod are present (i.e., excluding seine hauls with no age 0 cod) in August, there is no significant relationship between density and eelgrass complexity, suggesting that differential survival may have influenced density patterns. However, in August of 2000, cod density increased linearly with

increasing habitat complexity. This indicates that high numbers of cod selectively recruited to areas of higher eelgrass complexity.

When data from all three years were combined and analyzed for each month, the relationship between cod density and eelgrass complexity was strong only for September. During this month sites with eelgrass of intermediate complexity contained the highest densities of age 0 cod. In all other months, a relationship was evident only in some years. In July, when age 0 cod densities were low (Table 3.3), no relationship was found between cod density and eelgrass complexity for any year. Relationships between cod density and eelgrass complexity for all other months and years were inconsistent, suggesting that factors other than habitat complexity may also be important in determining the distribution of cod. Biological processes such as predation and food availability affect mortality rates and distribution patterns in periods within the year when there is no new recruitment (Tupper and Boutilier 1995, Linehan et al. 2001).

In September, the age 0 cod population is somewhat stable in Newman Sound (i.e., no new recruitment is occurring), and cod densities are highest at sites with intermediate eelgrass complexity. Several authors have suggested that patchy seagrass coverage is better than a meadow of seagrass. Tupper and Boutilier (1995) found that postsettlement survival and subsequent juvenile cod densities were higher in more structurally complex habitats, mainly due to increased shelter availability and decreased predator efficiency within these habitats. Irlandi et al. (1995) suggested that unvegetated sediments associated with patchy seagrass coverage may serve as corridors facilitating

Table 3.3: Mean density (#/seine haul/month or #/seine haul/year) of age 0 cod in Newman Sound for July, August, September, October and November of 1998, 1999, and 2000 (number of seine hauls in parentheses).

Month	**1998 density**	**1999 density**	**2000 density**	**All years Σ**
July	4.87 (7)	0.22 (12)	6.00 (12)	**3.51**
August	106.86 (16)	109.73 (12)	8.47 (12)	**78.20**
September	25.30 (23)	156.33 (12)	31.42 (12)	**60.32**
October	37.67 (15)	97.17 (12)	17.42 (12)	**49.74**
November	2.77 (13)	36.00 (12)	13.92 (12)	**17.16**
Σ	**39.55**	**79.89**	**15.44**	-

the movement into and among seagrass patches of large mobile organisms. Orth et al. (1984) stated that heterogeneous grass beds (bare sand areas interspersed within the bed) should provide more favorable foraging areas for mobile fishes or invertebrates. This is because mobile fish or invertebrates, particularly juveniles, may forage over the unvegetated areas while at the same time remaining in close proximity to their protective vegetated habitat (Orth et al. 1984). Moreover, a diel pattern has been suggested: fish use vegetation as a shelter by day and forage over sand under protection of night (Orth et al. 1984, Borg et al. 1997). Linehan et al (2001) found that predation on tethered prey (age 0 cod) was lower at night than during day and dusk regardless of habitat and depth. Holt et al. (1983) hypothesized that observed patterns in seagrasses were related to juvenile fishes' (red drum, *Sciaenops ocellatus*) requirements for open feeding areas with simultaneous protection from large predators. Thus, patchy areas with a high percentage of edges or "ecotones" may actually support a higher density of some mobile foraging species than homogeneous areas.

Why would a high complexity site, such as South Broad Cove (D_f = 1.3625) not support the same densities as a site with an intermediate D_f? I suggest the perimeter to area ratio can be too high. Even though more cod are caught at South Broad Cove than several of the lower complexity sites, it may be inferior to intermediate complexity sites because the corridors between patches of eelgrass are too large, or the patches themselves are too small. Irlandi (1997) states that small patches have greater edge to area ratios than large patches, theoretically making prey more available to predators. In a study on the effects of eelgrass habitat edge on predation on age 0 cod, Gorman (2002) found the edge

to be more dangerous than the surrounding mud and eelgrass habitats and that risk decreases with increasing distance from the edge. Orth (1992) suggests that prey abundances will be a balance between refuge from predation and the availability of increased space.

Physical factors such as depth, salinity, and level of exposure may have a larger impact on cod densities during unstable times for the nearshore population (i.e., during recruitment pulses or when cod are moving offshore due to cooling water temperatures). These factors may influence where cod settle more than biological factors such as presence or absence of predators. Biological factors (e.g., predation, competition) almost certainly play a role during recruitment pulses as well, but evidence of such processes is less obvious when cod are in a state of flux. Godo et al. (1989) found that cod settled mainly in shallow (0-100 m) sheltered areas and were absent at the most exposed locations and in deep water. In a preliminary analysis, I found that fractal dimension of eelgrass habitat may be inversely related to depth. From this, it may be speculated that age 0 cod may prefer complex eelgrass at deeper sites rather than low complexity at shallow depths.

Other factors that may affect eelgrass complexity and the presence or density of age 0 cod are salinity, substrate, and level of exposure. Riley and Parnell (1984) suggested that there is a negative relation between juvenile cod and salinity; however, Methven et al. (1997) did not find such a relationship to be significant in similar tests in Newfoundland. Several investigators have shown the importance of substrate to juvenile cod (Lough et al. 1989, Gotceitas and Brown 1993, Gotceitas et al. 1995, Tupper and

Boutilier 1995, Fraser et al. 1996, Gotceitas et al. 1997, Gregory and Anderson 1997). In the laboratory, age 0 cod are capable of assessing risk of predation and actively select habitat where predator risk was lowest (Gotceitas et al. 1997). Level of wind or wave exposure at a site indirectly affects cod densities due to the impact it has on eelgrass habitat. Ings et al. (in prep.) found that areal extent of eelgrass increases with complexity of the coastline which they argue is a measure of level of exposure. They also found that cod abundance increases with coastline complexity, due to the relationship between coastline complexity and eelgrass areal extent.

The distribution and density of age 0 cod are undoubtedly affected by a number of factors, both biological and physical. In providing a multi-scale measure of habitat complexity for a preferred habitat of this species, I have provided an answer to one more question that we have about cod ecology: cod are more likely to be found associated with eelgrass habitat high in complexity, but the relationship between cod density and eelgrass complexity is strong only when cod are not moving into or out of the nearshore environment. Clearly, more investigation is required into factors such as predator/prey relationships, inter- and intra-specific competition and food availability. This will provide more insight into density and distribution patterns of age 0 cod. Future studies should also investigate the mechanisms - physical, geological, and chemical - that cause varying degrees of eelgrass complexity in Newfoundland. As with any ecological study, investigators should realize the importance of performing studies at scales appropriate to the questions being posed.

3.5 Acknowledgements

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Chapter 4: Summary

4.1 Scaling in ecology

Ecology is a scale-based science (Wiens 1989; Levin 1992), whether we choose to incorporate scale or not. This concept is becoming more recognized in ecological studies (Schneider 2001) as investigators realize that ecological processes operating at large scales are not always the same as those operating at small scales (Thrush et al. 1997). However, fine-scale measurements are often extrapolated to broader-scale phenomena (Turner 1990). Information is lost as spatial data are considered at coarser scales of resolution (Schneider and Piatt 1986; Turner 1990). Developing methods to preserve information across scales is a critical task (Turner 1990). However, in order to determine scale-dependent effects of ecological processes, we need to know how to interpret data and reliably extrapolate results across multiple scales (Gardner 1998). The best way to determine whether extrapolations are reliable is to first predict, and then test these extrapolations. In Chapter 2, I hypothesized that it would be possible to extrapolate between analyses of eelgrass habitat measurements collected at different scales. This was possible when lateral heterogeneity of eelgrass habitat was not a seriously confounding problem.

Seagrass habitat structure varies spatially (Robbins and Bell 1994; Irlandi et al. 1995; Turner et al. 1999) and temporally (Olesen and Sand-Jensen 1994). The measurement of spatial pattern and heterogeneity is dependent upon the scale at which measurements are made (Turner 1989). I have shown that scaling laws can be determined

for eelgrass habitat, and these laws can be extended between small (underwater video transect lines) and large (aerial photographs) resolutions. Simply adding or multiplying the effects identified in small scale analyses would have been inaccurate. This is because summing of small scale processes does not allow the prediction of larger scale effects (Thrush et al. 1997).

The resolution at which a single-scale study is conducted often depends on the background and viewpoint of the investigator, as well as the problem that is being investigated (Farmer and Adams 1991). Which spatial scales are appropriate for studies of the association between juvenile cod and eelgrass habitat? Certainly juvenile cod are associated with eelgrass at small scales (i.e., size of a patch) for predator refuge, and possibly even smaller scales (e.g., eelgrass blades, rhizomes) due to feeding requirements. However, juvenile cod distributions and densities may be related to eelgrass habitat at the scale of coves, sounds, bays, or even coastlines. Syms (1995) discusses how oceanographic, geological, and physical factors all act on fish assemblages and population structure at different scales. Finding an appropriate 'scale' of sampling should be less important than multi-scale modeling and sampling, which may provide us with an increased ability to detect and interpret large-scale relationships (Hewitt et al. 1998).

4.2 Are eelgrass systems true fractals?

Fractals can be used to describe the complexity of natural patterns and the changes in these patterns with changes in scale (Gardner 1998). While a true fractal is an

infinite mathematical set, natural objects are finite, being limited by some fundamental building block (Johnson et al. 1995). Nevertheless, fractal geometry provides a more realistic characterization of naturally occurring objects, such as habitat, when compared to classical Euclidean geometry (Johnson et al. 1995). Palmer (1988) suggests that vegetation is a prime example of a fractal because it has detail at all spatial scales of interest.

The key idea in fractal geometry is self-similarity (Hastings and Sugihara 1993). This can be detected by determining whether the fractal dimension (D_f) shifts with changes in scale (Burrough 1981). A constant value of D_f at different spatial scales indicates a self-similar pattern, and any portion of the sample provides an adequate statistical representation of the whole (Gardner 1998). Self-similarity disappears when the value of D_f shifts with changes in scale, indicating that the patterns seen are dependent on the scale of measurement (Gardner 1998). Most natural objects do not display exact self-similarity but display some degree of 'statistical' self-similarity, at least over a limited range of spatial scales (Kenkel and Walker 1996). In any case, statistical self-similarity is not a prerequisite to applying fractal concepts (Kenkel and Walker 1996). Strictly speaking, eelgrass systems are not true fractals but eelgrass habitat complexity can be described using fractal analyses over a limited range of resolutions (see Chapter 3).

Many natural fractal-like structures (e.g., vegetation) are determined by a large number of generating processes operating at different scales (Scheuring and Riedi 1994). Such structures (termed multifractals) are characterized by fractional dimensions that

vary with scale, and so require an infinite number of scaling exponents for their description (Kenkel and Walker 1996). Instead of incorporating multifractals, I chose a limited range of resolutions and applied a quadratic formula to eelgrass data from transect lines to compare with eelgrass data from aerial photographs (see Chapter 2). This simplified procedure allowed a direct comparison of parameters from each method. In addition, this allowed me to simplify to a linear model if values of D_f^2 were not significant (e.g., see Figure 2.4).

4.3 Applications for the future

My thesis was, first, that eelgrass measurements could be scaled from small to large using two different methods; and second, that cod densities are influenced by eelgrass complexity in Newman Sound, as measured by fractal analyses. Few studies have been done on eelgrass habitat in Newfoundland, although it is known to be important to cod distributions (Gotceitas et al. 1997; Ings et al. in prep.). Understanding the mechanisms that contribute to varying degrees of eelgrass complexity and the distribution and densities of juvenile cod are important next steps.

It is highly suggested that eelgrass habitat complexity be quantified at even larger scales; in particular, the entire east coast of Newfoundland must be quantified because this is the scale at which recruitment occurs. The standard way of incorporating scale in ecological research is to define subsystems and relate them to the system as a whole (Allen and Starr 1982; O'Neill et al. 1986). The scaling relationship between eelgrass complexity at sites in Newman Sound and sites along Newfoundland's east coast could

be determined. Cod density data exists from 1992-1997 at 36-45 sites along the east coast from Fleming survey data (Methven et al. 1998). The relationship between cod density patterns and eelgrass complexity could be investigated on an even larger scale, furthering our understanding of juvenile cod ecology.

Finally, concepts from my study can also be applied to other aspects of juvenile cod ecology. For example, predation rates on juvenile cod in Newman Sound have been calculated with respect to eelgrass habitat edge at small scales (e.g., the size of a patch) (Gorman 2002). Predictions could be made about these relationships at larger scales (e.g., the size of a cove). By computing a scaling law for the amount of edge using aerial photography, it may be possible to calculate predation rates at larger scales. These predictions could then be tested by direct measurements in the field.

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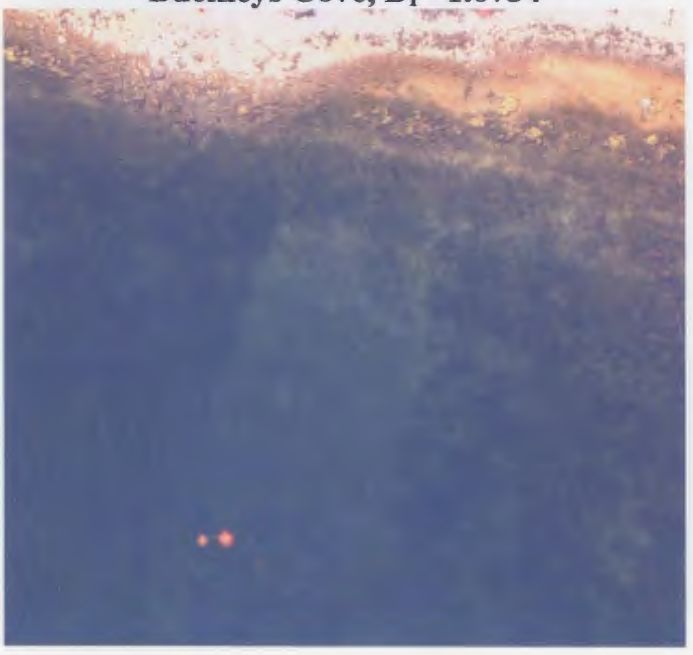
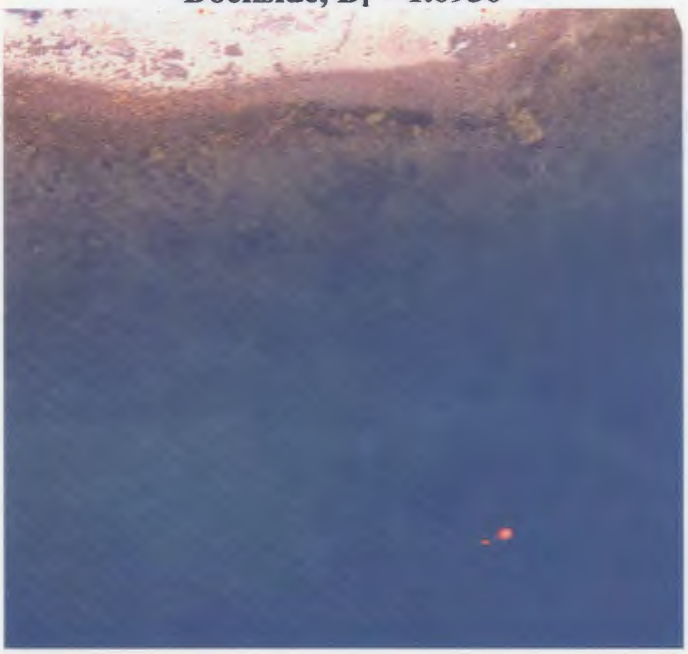
Appendix 1: Aerial photographs of 8 sites in Newman Sound, Newfoundland, taken in August 2000. Fractal dimensions (D_f) given for each site as an index of complexity for eelgrass.

Big Brook, $D_f = 1.0$

Buckleys Cove, $D_f = 1.0754$

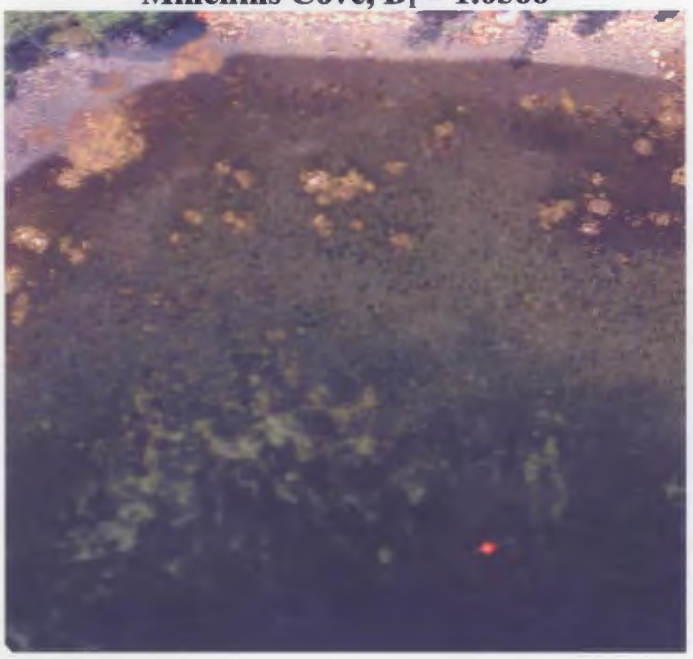


Dockside, $D_f = 1.0930$



Hefferns Cove, $D_f = 1.1013$

Minchins Cove, $D_f = 1.0566$



Mistaken Cove, $D_f = 1.1649$

South Broad Cove, $D_f = 1.3625$

White Rock, $D_f = 1.1565$

Appendix 2: Example (using Big Brook data) of test for lateral heterogeneity between eelgrass habitat over 3 transect lines.

Model:
$\log A = \beta_o + \beta_{logR} * \log R + \beta_L * L$

Symbols:
$\log A = \log_{10}$ area
$\log R = \log_{10}$ resolution (i.e. box size, m^2)
L = transect line (class variable: left, middle or right)

Results:

```
Class: L
Levels: 3
Values: 1 2 3
Number of observations: 18
Dependent Variable: logA
```

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	0.06105989	0.02035330	146.46	<.0001
Error	14	0.00194558	0.00013897		
Corrected Total	17	0.06300547			

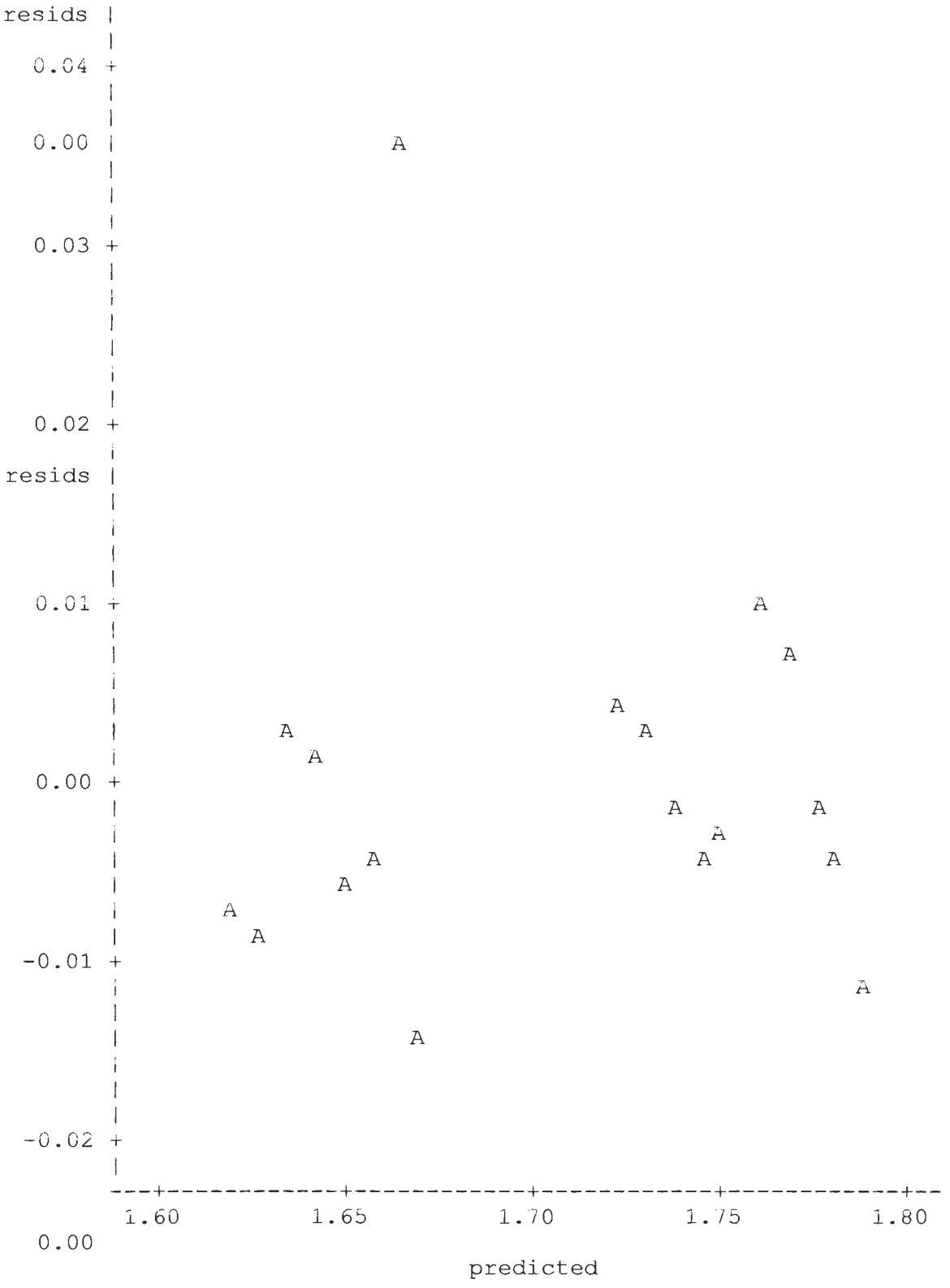
R-Square	Coeff Var	Root MSE	logA Mean
0.969120	0.690639	0.011789	1.706906

Source	DF	Type III SS	Mean Square	F Value	Pr > F
logR	1	0.00308177	0.00308177	22.18	0.0003
L	2	0.05981979	0.02990990	215.23	<.0001

Parameter		Estimate		Standard Error	t Value	Pr > |t|
Intercept		1.782488528	B	0.00549931	324.13	<.0001
logR		0.021684898		0.00460488	4.71	0.0003
L	1	-0.140201480	B	0.00708453	-19.79	<.0001
L	2	-0.038140000	B	0.00745574	-5.12	0.0002
L	3	0.000000000	B	.	.	.

Therefore the regression equation is:
$\log A = 1.782 + 0.02168 * \log R + \beta_L * L$
(where $\beta_{L1} = -0.1402$, $\beta_{L2} = -0.03814$ and $\beta_{L3} = 0.0000$)

Plot of resids*predicted. Legend: A = 1 obs, B = 2 obs, etc.



Appendix 3: Example (using Minchins Cove data) of complete analysis for comparing eelgrass measurements from underwater video transect lines to eelgrass measurements from aerial photographs.

Model:
$\log P = \beta o + \beta_{logR1} * logR1 + \beta_{logR2} * logR2 + \beta_M * M$

Symbols:
logP = $\log_{10}$ perimeter
logR1 = $\log_{10}$ resolution (i.e. length of side of box, m)
logR2 = $\log_{10}$ resolution squared
M = method (class variable: Ma = aerial photography and Mu= underwater video)

Results:

```
Class: M
Levels: 2
Values: 1 2
Number of observations: 16
Dependent Variable: logP
```

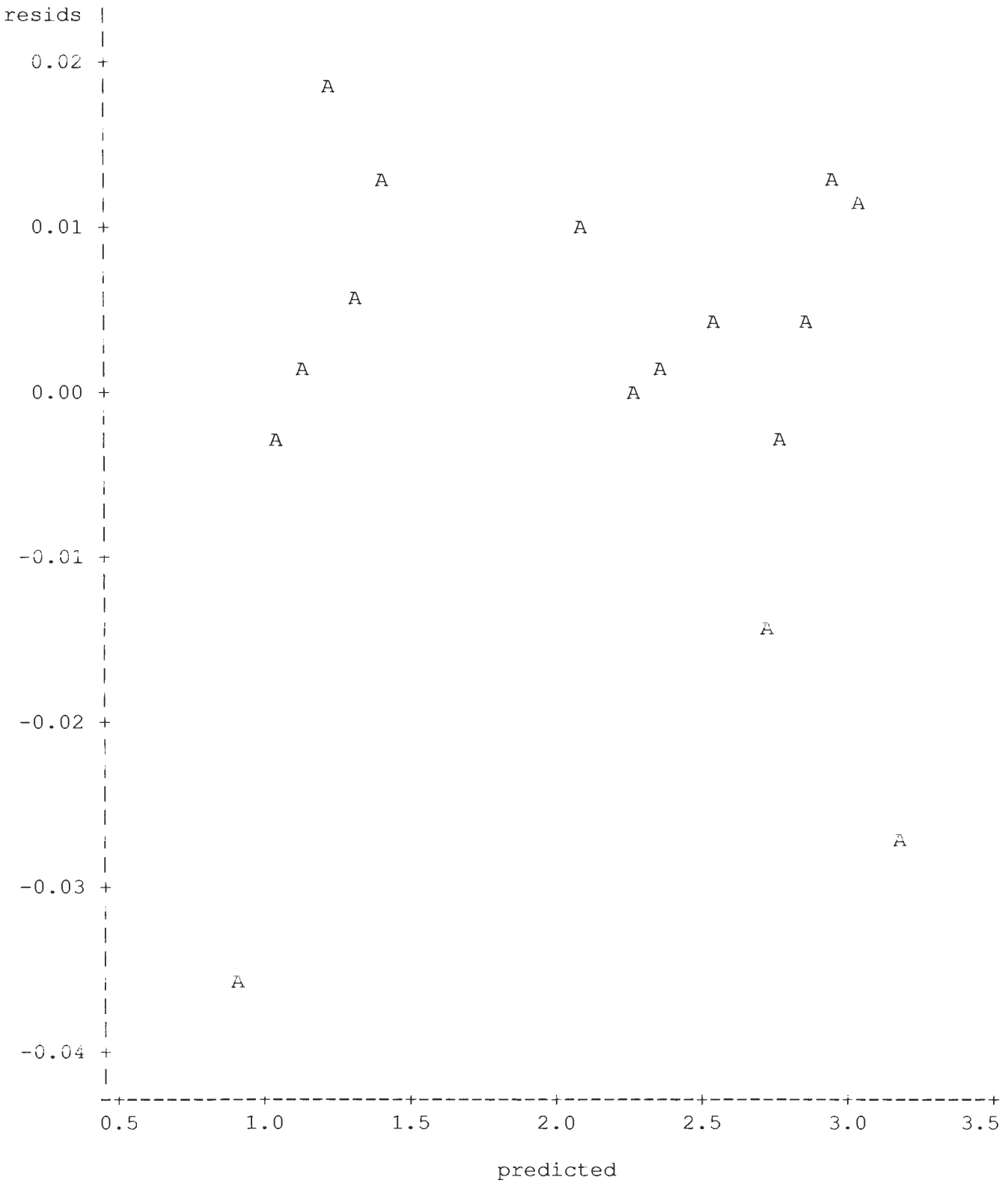
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	9.76046761	3.25348920	12060.6	<.0001
Error	12	0.00323715	0.00026976		
Corrected Total	15	9.76370476			

R-Square	Coeff Var	Root MSE	logP Mean
0.999668	0.778283	0.016424	2.110344

Source	DF	Type III SS	Mean Square	F Value	Pr > F
logR1	1	0.03303913	0.03303913	122.47	<.0001
logR2	1	0.02744709	0.02744709	101.75	<.0001
M	1	9.29650857	9.29650857	34461.8	<.0001

Parameter		Estimate	Standard Error	t Value	Pr > |t|
Intercept		3.175964969 B	0.01263249	251.41	<.0001
logR1		-0.397615198	0.03592854	-11.07	<.0001
logR2		-0.238234561	0.02361824	-10.09	<.0001
M	1	-1.709494517 B	0.00920871	-185.64	<.0001
M	2	0.000000000 B	.	.	.

Therefore the regression equation is:
$\log P = 3.176 - 0.3976 * logR1 - 0.2382 * logR2 + \beta_M * M$
(where $\beta_{Ma} = 0.000$ and $\beta_{Mu} = -1.710$)


Plot of resids*predicted. Legend: A = 1 obs, B = 2 obs, etc.
resids
0.02
0.01
0.00
-0.01
-0.02
-0.03
-0.04
0.5
1.0
1.5
2.0
2.5
3.0
3.5
predicted

Appendix 4: Example of complete analysis for determining relationship between proportion of successful seine hauls with age 0 cod and eelgrass habitat complexity (using all months and all years).

Model:

$P = \beta o + \beta_{Df} * Df + \beta_M * M$

Symbols:

P = perimeter
Df = fractal dimension of eelgrass
M, Month = month (class variable: 1 = July, 2 = August and so on)
Total = total number of seine hauls
Success = number of seine hauls with age 0 cod

Results:

```
Distribution: Binomial
Link Function: Logit
Response Variable (Events): success
Response Variable (Trials): total
Observations Used: 30
Number Of Events: 147
Number Of Trials: 175
Class: month
Levels: 5
Values: 1 2 3 4 5
```

Analysis Of Parameter Estimates

Parameter		DF	Estimate	Standard Error	Wald 95% Confidence Limits		Chi-Square
Intercept		1	-2.3186	2.6756	-7.5627	2.9256	0.75
month	1	1	-2.5895	0.8355	-4.2271	-0.9519	9.61
month	2	1	-1.4772	0.8375	-3.1186	0.1642	3.11
month	3	1	-0.2378	0.9492	-2.0983	1.6227	0.06
month	4	1	-0.3749	0.9521	-2.2409	1.4912	0.16
month	5	0	0.0000	0.0000	0.0000	0.0000	.
Df		1	4.5433	2.3384	-0.0399	9.1264	3.77
Scale		0	1.0000	0.0000	1.0000	1.0000	

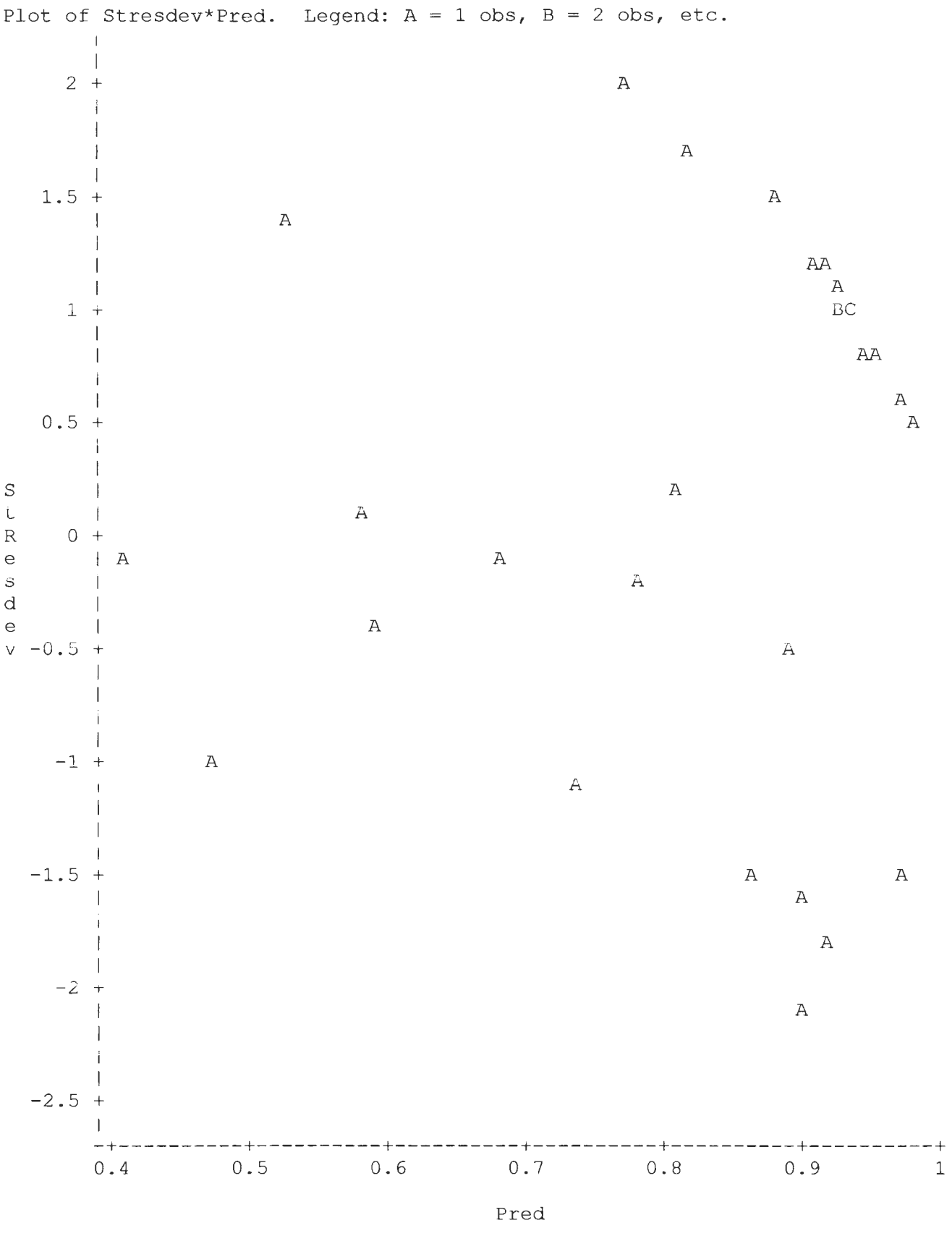
LR Statistics For Type 3 Analysis

Source	DF	Chi-Square	Pr > ChiSq
month	4	20.70	0.0004
Df	1	4.37	0.0366

Therefore the regression equation is:

$P = e^{(-2.32 + 4.54*Df + \beta M*M)} / [1 + e^{(-2.32 + 4.54*Df + \beta M*M)}]$

(where $\beta_{M1} = -2.5895$, $\beta_{M2} = -1.4772$, $\beta_{M3} = -0.2378$, $\beta_{M4} = -0.3749$, and $\beta_{M5} = 0.0000$)


Plot of Stresdev*Pred. Legend: A = 1 obs, B = 2 obs, etc.
Stresdev
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
0.4
0.5
0.6
0.7
0.8
0.9
1
Pred

Appendix 5: Example of complete analysis for determining relationship between density of age 0 cod when present and eelgrass habitat complexity (using September data, all three years).

Model:
$C = \beta o + \beta_{Df} * Df + \beta_{Df2} * Df2$

Symbols:
C = age 0 cod density
Df = fractal dimension of eelgrass
Df2 = fractal dimension squared

Results:

```
Distribution: Gamma
Link Function: Log
Dependent Variable: count
Observations Used: 44
```

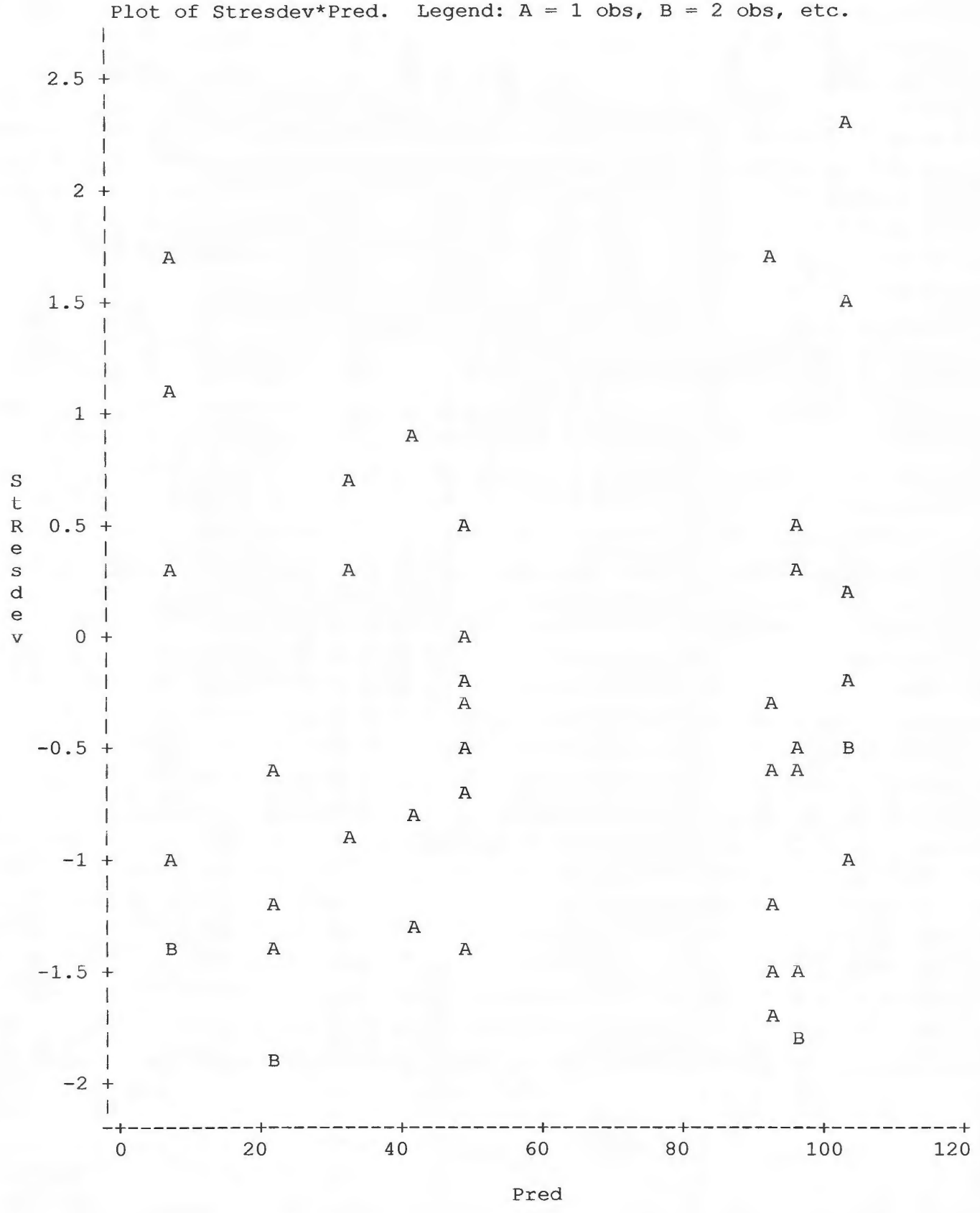
Analysis Of Parameter Estimates

Parameter	DF	Estimate	Standard Error	Wald 95% Confidence Limits		Chi-Square	Pr>ChiSq
Intercept	1	-70.5019	16.5480	-102.935	-38.0685	18.15	<.0001
Df	1	120.1075	28.2093	64.8183	175.3966	18.13	<.0001
Df2	1	-47.7304	11.9440	-71.1401	-24.3207	15.97	<.0001
Scale	1	0.8137	0.1499	0.5671	1.1676		

LR Statistics For Type 3 Analysis

Source	DF	Chi-Square	Pr > ChiSq
Df	1	13.39	0.0003
Df2	1	11.98	0.0005

Therefore the regression equation is:
$C = (e^{-70.502}) \cdot (e^{120.11 \cdot D_f}) \cdot [e^{-47.730 \cdot (D_f^2)}]$


Plot of Stresdev*Pred. Legend: A = 1 obs, B = 2 obs, etc.
StResdev
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
0
20
40
60
80
100
120
Pred

Appendix 6: Results (p values and residual checks) for analyses of relationship between 1998, 1999 and 2000 cod densities and fractal dimension of eelgrass habitat.

M	Y	Model	M	Y	D_f	D_f^2	$M*D_f$	$M*D_f^2$	$Y*D_f$	$Y*D_f^2$	Residuals
All	All	$C = M + Y + D_f + D_f^2 + M*D_f + M*D_f^2 + Y*D_f + Y*D_f^2 + \varepsilon$	0 1248	0 3033	0 0149	0 0152	0 1520	0 1812	0 3184	0 3274	Not normal
All	All	$C = M + Y + D_f + D_f^2 + M*D_f + Y*D_f + \varepsilon$	0 0544	0 8594	0 0060	0 0067	0 0413		0 8411		Not normal
All	All	$C = M + Y + D_f + D_f^2 + M*D_f^2 + Y*D_f^2 + \varepsilon$	0 0666	0 7853	0 0057	0 0064		0 0520		0 8652	Not normal
All	All	$C = Y + D_f + D_f^2 + Y*D_f + Y*D_f^2 + \varepsilon$		0 0729	0 0014	0 0018			0 0778	0 0782	Ok
All	All	$C = M + D_f + D_f^2 + M*D_f + M*D_f^2 + \varepsilon$	0 0556		0 0887	0 0921	0 0707	0 0857			Ok
All	All	$C = M + D_f + D_f^2 + M*D_f^2 + \varepsilon$	0 0106		0 0241	0 0280		0 0029			Ok
All	All	$C = M + D_f + D_f^2 + M*D_f + \varepsilon$	0 0052		0 0268	0 031	0 0023				Ok
July	All	$C = Y + D_f + D_f^2 + Y*D_f + Y*D_f^2 + \varepsilon$		0 0134	0 5711	0 4906			0 0112	0 0086	Not normal
July	1998	$C = D_f + D_f^2 + \varepsilon$			0 0338	0 0276					Not normal
July	1998	$C = D_f + \varepsilon$			0 0233						Not normal
July	1999	$C = D_f + D_f^2 + \varepsilon$			0 1405	0 1363					Ok
July	1999	$C = D_f + \varepsilon$			0 6997						Not normal
Aug	All	$C = Y + D_f + D_f^2 + Y*D_f + Y*D_f^2 + \varepsilon$		0 4995	0 3456	0 3215			0 4445	0 3991	Ok
Aug	All	$C = D_f + D_f^2 + \varepsilon$			0 3643	0 3202					Ok
Aug	1998	$C = D_f + D_f^2 + \varepsilon$			0 6446	0 6423					Ok
Aug	1998	$C = D_f + \varepsilon$			0 9589						Ok
Aug	1999	$C = D_f + D_f^2 + \varepsilon$			0 2256	0 1648					Not normal
Aug	1999	$C = D_f + \varepsilon$			0 0006						Ok
Aug	2000	$C = D_f + D_f^2 + \varepsilon$			0 5202	0 5201					Not normal
Aug	2000	$C = D_f + \varepsilon$			0 9969						Not normal
Sept	All	$C = Y + D_f + D_f^2 + Y*D_f + Y*D_f^2 + \varepsilon$		0 2062	<0 0001	<0 0001			0 2411	0 2669	Ok
Sept	All	$C = D_f + D_f^2 + \varepsilon$			0 0003	0 0005					Ok
Oct	All	$C = Y + D_f + D_f^2 + Y*D_f + Y*D_f^2 + \varepsilon$		0 2174	0 0494	0 0511			0 2386	0 2508	Ok
Oct	All	$C = Y + D_f + Y*D_f + \varepsilon$		0 6540	0 8000				0 7272		Not normal
Oct	All	$C = D_f + D_f^2 + \varepsilon$			0 6493	0 6574					Ok
Oct	1998	$C = D_f + D_f^2 + \varepsilon$			0 3649	0 3579					Not normal
Oct	1998	$C = D_f + \varepsilon$			0 6801						Ok
Oct	1999	$C = D_f + D_f^2 + \varepsilon$			0 7183	0 7325					Ok
Oct	1999	$C = D_f + \varepsilon$			0 7175						Ok
Oct	2000	$C = D_f + D_f^2 + \varepsilon$			0 0353	0 0375					Ok

Appendix 6 cont'd: Results for analyses of relationship between 1998, 1999 and 2000 cod densities and fractal dimension of eelgrass habitat.

M	Y	Model	M	Y	D_f	D_f^2	M*D_f	M* D_f^2	Y*D_f	Y* D_f^2	Residuals
Oct	2000	$C = D_f + \varepsilon$			0 4798						Ok
Nov	All	$C = Y + D_f + D_f^2 + Y*D_f + Y* D_f^2 + \varepsilon$		0 9555	0 0349	0 0262			0 9845	0 9945	Not normal
Nov	All	$C = D_f + D_f^2 + \varepsilon$			0 2930	0 2381					Not normal
Nov	1998	$C = D_f + D_f^2 + \varepsilon$			0 0072	0 0064					Ok
Nov	1998	$C = D_f + \varepsilon$			0 343						Not normal
Nov	1999	$C = D_f + D_f^2 + \varepsilon$			0 2964	0 2415					Not normal
Nov	1999	$C = D_f + \varepsilon$			0 0429						Ok
Nov	2000	$C = D_f + D_f^2 + \varepsilon$			0 2598	0 2493					Not normal
Nov	2000	$C = D_f + \varepsilon$			0 5567						Ok

C = cod density; M = month; Y = year; D_f = fractal dimension of eelgrass habitat; ε = error term